ECOLOGICAL STUDIES ON EXPLOITED POPULATIONS OF WHALES AND ROCK LOBSTERS

BY

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for the degree of Doctor of Science

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"Perhaps biologists have been content to
state the existence of density dependence
rather than measure it."

D.H. Cushing, 1974.

CONTENTS

PREFACE

The substance of this thesis is a collection of papers reporting research carried out by the author while a member of C.S.I.R.O. Division of Fisheries and Oceanography. While that Division is not responsible for fisheries management, it carries out research upon commercially important species as a backdrop to management needs.

Regulation of humpback whaling in Australia was primarily the responsibility of the Commonwealth Government and as the management authority at that time had little expertise in biology, the Division of Fisheries and Oceanography was more directly involved in management than usual. The author was a member of the Scientific Committee of the International Whaling Commission during the difficult period when the concept of managing individual populations of whales as discrete entities was being pressed upon those mainly concerned with commercial production from the southern waters as a whole.

In the case of the western rock lobster, the Western Australian Department of Fisheries and Wildlife, as the management authority, has built up its own expertise in fisheries management. In supporting the work of that Department, the Division of Fisheries and Oceanography carried out basic studies upon the physiology, behaviour and ecology of this species, as well as upon the oceanic circulation of the area. The author's contribution has been concerned mainly with aspects of ecology.

Papers 1,2,3 and 5 constituted part of a thesis for the degree of Doctor of Philosophy, conferred by the University of Western Australia in 1956. They are included here to give continuity to the studies on the humpback whale.

Paper 4 and 6 to 29, which constitute the present thesis, contain no material which has been accepted for the award of any other degree in any university. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person, except when due reference is made in the text of the thesis.

With regard to those papers having co-authors: in papers 6 and 16 the co-author was my technician. For both papers I was responsible for planning the work, for analysis and interpretation of the results, and for writing the manuscript. For paper 15, my colleague and I shared equally in this work. In paper 23, the section on larval settlement was contributed by B.F. Phillips; I was responsible for the work on juveniles and recruitment to the fishery. After discussing the results, I wrote the first draft of the paper.

Any other assistance, suggestions or criticisms are acknowledged at the end of the relevant paper.

R.G. CHITTLEBOROUGH

INTRODUCTION

The humpback whale and the western rock lobster are widely separated in phylogeny, morphology and physiology. At first sight they have little in common except a marine habitat. Both have a relatively high longevity and when undisturbed appear to attain fairly stable population levels determined by responses to environmental pressures. However, in most other respects their life cycles differ greatly, as shown by the summary in Table 1.

Despite these differences, when populations of either species are exploited commercially, a similar rationale is applied to management. Compensatory changes are expected to occur to some extent in birth rate, growth rate, and/or survival as the population is reduced (usually selectively) from some maximal level. Where the interactions of these parameters are optimised giving greatest recruitment to the fishable stock, a fishery can be continued indefinitely at a level classically known as the maximum sustainable yield. Thus in spite of the widest of differences between these species, the responses of their populations to fishing pressure are expected to be similar in principle if not in extent.

The research upon humpback whales is brought together in paper 14, while the implications of the findings on the western rock lobster are discussed in paper 26. Following the presentation of research papers, the above hypothesis is examined in the light of data collected from populations of humpback whales and the western rock lobster as these were exposed to high rates of exploitation.

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TABLE 1

COMPARATIVE FEATURES OF LIFE CYCLE IN HUMPBACK WHALE AND WESTERN ROCK LOBSTER

Life Cycle	Humpback whale	Western rock lobster
Fertilisation	internal	external
Gestation (incubation)	11½ months temp. independent	19-68 days temp. dependent
Fecundity	low 1 calf in 2·7 yrs.	high at least 1 brood (300,000 larvae) per yr.
Length at birth	427 cm.	0.12 cm.
Maternal care of young	intense	none
Juvenile mortality	low	very high
Post-natal habitat	oceanic (as for parents)	oceanic planktonic larvae (shelf benthic parents)
Duration of:--		
suckling phase	10½ months	
larval phase		9-11 months
Age at 1st. breeding (female)	4-5 years	7-8 yrs. in parts of wild population. 3-6 yrs. in aquarium
Feeding	seasonal (Antarctic summer) Euphausia only	daily for optimum growth. Diverse species
Homogeneity of population	continual mixing within each population	mixing and dispersion across geographic range only during larval phase: restricted home range in juveniles; possibly in adults
Longevity	20+ years (maximum 48 yrs.)	Maximum probably over 15 years

LIST OF PAPERS

A. THE HUMPBACK WHALE

* 1. Aspects of reproduction in the male humpback whale. _Aust. J. Mar. Freshw. Res._ 6(1): 1-29.

* 2. Studies on the ovaries of the humpback whale on the Western Australian coast. _Aust. J. Mar. Freshw. Res._ 5(1): 35-63.

* 3. Puberty, physical maturity, and relative growth of the female humpback whale on the Western Australian coast. _Aust. J. Mar. Freshw. Res._ 6(3): 315-327.

4. The breeding cycle of the female humpback whale. _Aust. J. Mar. Freshw. Res._ 9(1): 1-18

* 5. Aerial observations on the humpback whale, with notes on other species. _Aust. J. Mar. Freshw. Res._ 4 (2): 219-226.

6. A review of whale marking and some trials of a modified whale mark. _Norsk. Hvalfangsttid._ 46(5): 238-248.

7. Australian marking of humpback whales. _Norsk. Hvalfangsttid._ 48(2): 47-55.

8. Intermingling of two populations of humpback whales. _Norsk. Hvalfangsttid._ 48(10): 510-521.

9. Determination of age in the humpback whale. _Aust. J. Mar. Freshw. Res._ 10(2): 125-143.

10. Marked humpback whale of known age. _Nature_ 187 (4732) :164.

11. An analysis of recent catches of humpback whales from the stocks in Groups IV and V. _Norsk. Hvalfangsttid._ 47(3): 109-137.

12. Apparent variations in the mean length of female humpback whales at puberty. _Norsk Hvalfangsttid._ 49(3): 120-124.

13. Licence limitation as applied to whaling. Fisheries Management Seminar, 1963 Rep. of Proceedings (Dept. Prim. Indust. Canberra)

14. Dynamics of two populations of the humpback whale, _Megaptera novaeangliae_ (Borowski). _Aust. J. Mar. Freshw. Res._ 16(1): 33-128.

* Thesis for degree of Doctor of Philosophy conferred by the University of Western Australia in 1956.

B. THE WESTERN ROCK LOBSTER

15. Preliminary assessments of stocks of the Western Australian crayfish, *Panulirus cygnus* George. *Aust. J. Mar. Freshw. Res.* 17: 93-121.

16. Larval ecology of the Western Australian marine crayfish, with notes upon other panulirid larvae from the eastern Indian Ocean. *Aust. J. Mar. Freshw. Res.* 20:199-23.

17. Studies on recruitment in the Western Australian rock lobster *Panulirus longipes cygnus* George: density and natural mortality of juveniles. *Aust. J. Mar. Freshw. Res.* 21:131-48.

18. Development of a tag for the western rock lobster. CSIRO Div. Fish. and Oceanogr. Rep. 56.

19. Western rock lobster reared to maturity. *Aust. J. Mar. Freshw. Res.* 25: 221-5.

20. Home range, homing and dominance in juvenile western rock lobsters. *Aust. J. Mar. Freshw. Res.* 25: 227-34.

21. Review of prospects for rearing rock lobsters. *Australian Fisheries.* 33(4): 1-5.

22. Environmental factors affecting growth and survival of juvenile western rock lobsters *Panulirus longipes* (Milne-Edwards). *Aust. J. Mar. Freshw. Res.* 26:177-96.

23. Fluctuations in year-class strength and recruitment in the western rock lobster *Panulirus longipes* (Milne-Edwards). *Aust. J. Mar. Freshw. Res.* 26: 317-28.

24. Growth of juvenile *Panulirus longipes cygnus* George, on coastal reefs compared with those reared under optimal environmental conditions. *Aust. J. Mar. Freshw. Res.* 27: 279-95.

25. Breeding of *Panulirus longipes cygnus* George under natural and controlled conditions. *Aust. J. Mar. Freshw. Res.* 27: 499-516.

26. Natural regulation of the population of *Panulirus longipes cygnus* George and responses to fishing pressure. ICES Special Meeting on Population Assessment of Shellfish Stocks, Copenhagen, 1976: Contribution No. 18.

C. MINOR SUPPORTING PAPERS

27. Southern right whale in Australian waters. *J. Mammalogy*. 37(3): 456-7.

28. *Balaenoptera brydei* Olsen on the west coast of Australia. *Norsk. Hvalfangsttid.* 48(2): 62-6.

29. The tropical rock lobster *Panulirus ornatus* (Fabr) as a resource in Torres Strait. CSIRO Div. Fish. and Oceanogr. Rep. 58.

Paper 1

RGChittleborough

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ASPECTS OF REPRODUCTION IN THE MALE HUMPBACK WHALE, *MEGAPTERA NODOSA* (BONNATERRE)

By R. G. Chittleborough

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Australia

ASPECTS OF REPRODUCTION IN THE MALE HUMPBACK WHALE, *MEGAPTERA NODOSA* (BONNATERRE)

By R. G. CHITTLEBOROUGH*

(*Manuscript received August 2, 1954*)

Summary

At puberty, male humpback whales off the Western Australian coast have an average body length of 36 ft 9 in. From histological examination of the testes, the extreme range of lengths at puberty is from 33 ft 4 in. to 40 ft 10 in. The mean testis weight at puberty is 2000 g. Following puberty, males are of low fertility for a period (possibly 1 yr) during which testis weight, tubule diameter, and spermatogenetic activity increase, before the attainment of full sexual maturity.

The mean length of the penis at puberty is 3.5 ft, but owing to considerable individual variation the penis length alone is not a reliable criterion of puberty. In sexually mature males the penis length ranges from 3.2 to 6.2 ft.

The proportion of fully physically mature males amongst those examined was very low (1.4 per cent.). The mean body length of those defined in this paper as approaching physical maturity was 41.90 ± 0.35 ft, and that of the fully physically mature males was 42.97 ± 1.59 ft. The largest male examined (46.42 ft) showed no sign of epiphysial fusion.

Changes in mean testis weight, mean diameter of testis tubules, and number of sperms in testes and vas deferens fluid have been followed at various stages of the life cycle. The variations of these characters in mature individuals have been examined for evidence of a seasonal cycle in male humpback whales; increasing testis weight and more active spermatogenesis are exhibited during winter months off Western Australia.

I. INTRODUCTION

In previous studies on the humpback whale and upon whales in general, the female reproductive cycle has received far more attention than have reproductive changes in the male.

The length of male humpback whales at puberty (an important characteristic in catch analyses) has not been accurately determined. In earlier research upon reproduction in whales (Mackintosh and Wheeler 1929; Matthews 1937, 1938*a*, 1938*b*; Nishiwaki and Oye 1948; Jonsgard 1951; Omura 1953) the term "sexual maturity," has been applied in a very general sense to mean that stage at which whales are capable of, and do effect, reproduction. In this paper it is intended to follow the procedure of Asdell (1946, p. 10), applying the term puberty to that stage at which reproduction first becomes possible, i.e. when germ cells are released, and confining the term sexual maturity to the time when the animal reaches

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its full reproductive power. It will be seen that in the male humpback whale there is a significant interval between these two events.

Matthews (1937) working on humpbacks, and Mackintosh and Wheeler (1929) on blue and fin whales, used testis "volume" to follow the increase in testis size with body length; their data showed a rapid increase in testis size at maturity. Matthews claimed that in humpback whales there was no correlation between testis size and body length after maturity.

Japanese workers (Omura 1953) have indicated that in humpback whales at "sexual maturity" the weight of testes is 2000 g, but Omura suggests that this figure may be too low as an index of "sexual maturity".

Matthews (1937) recorded a penis length of 1.25-2.5 m in mature humpback whales. Mackintosh and Wheeler (1929) state that in blue and fin whales the penis undergoes considerable growth at "sexual maturity" and suggested that the size of the penis might be a useful index of the state of maturity.

Little information is available upon physical maturity in male humpback whales. Matthews recorded the state of the epiphyses of 12 males, three of which were approaching physical maturity.

While Mackintosh and Wheeler noted great enlargement of the testis tubules in blue and fin whales at maturity, no actual tubule diameters were given. Changes in the size of testis tubules from late foetal stages until after maturity have not been followed in whales.

Some indication of a male sexual season in humpback whales was noted by Matthews (1937), who found no spermatozoa in the testes of four mature males taken off South Georgia (Antarctica) in December-March but some sperms in the testes of three males taken off South Africa in July and August. Mackintosh and Wheeler (1929) also found indications of a similar breeding cycle in male blue and fin whales. They found very few sperms in testis tubules all the year round, but more in May, suggesting a male sexual season of April to June. Using testis "volume" they found no evidence of an increase in testis size during the breeding season. Engle (1927) found no sperms or spermatida in the testes of three male humpback whales at Trinidad, California, in August, and suggested a seasonal sexual cycle in the northern Pacific with breeding occurring during the winter months.

It is now possible to review the evidence of a male sexual season in humpback whales using such criteria as testis weight, diameter of testis tubules, spermatozoa in the testis, and variations of sperm density in vas deferens fluid.

This material was collected at Western Australian shore stations during the catching seasons (between June and early October) from 1951 to 1953.

II. METHODS

In this investigation, testis weight was used as a more precise index of testis development than the estimated volume used by Mackintosh and Wheeler (1929) and by Matthews (1937). Each testis was weighed after removing the epididymis and attached membranes. There was little difference in weight between the left and the right testis. In each whale the mean weight of the left and right testes was recorded. These mean testis weights of individuals and not the total weight of the testis pair are used throughout this paper.

When considering the testis weights of specified groups of males it was found that the distribution of mean testis weights within each group was unimodal and positively skewed; hence the geometric mean of the individual mean testis weights rather than the arithmetic mean was used as providing the better estimate of the mean for each group.

Samples of testis tissue were fixed in Heidenhain's Susa fixative or in formol-saline, sectioned at 7 μ and stained with haematoxylin and eosin. Although the whales had almost invariably been dead for at least 3 hr before tissues could be preserved, fair histological detail could be obtained, even in those dead for 8 or 9 hr.

During the histological examination of each testis sample, the diameters of 20 seminiferous tubules were measured with an ocular micrometer and the (arithmetic) mean diameter of the tubules obtained. Also the average number of sperms per tubule section (7 μ thick) was found after counting the sperms in 20 tubule sections.

Samples of fluid were collected from the vasa deferentia of relatively fresh whales (dead 3-6 hr). A 2 ml sample of fluid was withdrawn from the vas deferens by means of a syringe and added to a tube containing 8 ml of 10 per cent. formol-saline (giving a 1 : 5 dilution of preserved material). The corked tube was rotated to ensure a free suspension of sperms and also rapid fixation, after which the cork was sealed with wax. Before carrying out sperm counts upon these specimens in the laboratory, each tube was horizontally rotated for 3 min to resuspend the sperms. A small sample was mounted on a Neubauer haemocytometer slide and the count made under a phase contrast microscope. In most samples it was not found necessary to dilute the material any further, but in a few, epithelial cells were so numerous that further dilution was necessary in order to distinguish the sperms.

The state of physical maturity of these whales was determined from examination of the vertebral epiphyses, those males having all epiphyses fused to their respective vertebrae being classified as physically mature. As described by Mackintosh and Wheeler (1929) and Wheeler (1930), epiphysial fusion in whales begins in caudal and cervical vertebrae, extending forwards from the caudals more rapidly than back from the cervicals, so that the last epiphyses to be fused to the centra are those in the anterior thoracic region.

After exposure of the vertebral column the stage of epiphysial fusion was found by the method described by Wheeler. In the unfused state, the line of pearly white cartilage could be easily seen, but when fusion was taking place it was difficult to distinguish cartilage. In such instances, a small chip of bone across the epiphysial junction was placed over a slot in the flensing deck and lightly tapped. If the specimen broke directly along the junction with a smooth (though undulating) surface, this was classified as unfused but close to the point of fusion. When fusion was complete, such a fragment broke irregularly with a rough spongy surface, seldom along the line of fusion. This method was checked histologically, the microscopic examination agreeing very closely with the field diagnosis. Whales in which epiphysial fusion had begun but had not extended throughout the vertebral column were classified as approaching physical maturity.

III. PUBERTY

(a) *Histological Examination of Testes*

As stated by Mackintosh (1942) histological examination of the testes is the only unfailing method of determining the sexual state of a male whale. Figure 1 shows the mean testis weights and body lengths of 101 male humpback whales whose testes were examined histologically and so could be classified as sexually immature, at puberty, or mature. Immature testes (Plate 1, Fig. 2) had all seminiferous tubules closed or a few with lumina but containing no dividing spermatocytes. In testes at puberty (Plate 1, Fig. 3) the majority of tubules were open and contained some spermatocytes while closed tubules were not uncommon. In testes from mature males (Plate 1, Fig. 4) all tubules were open and various stages of spermatogenesis could be observed.

Figure 1 indicates that there is a wide range in body length at puberty, the extreme range being from 33 ft 4 in. to 40 ft 10 in. Hence it would be impossible to classify individual males as sexually immature or mature on the basis of body length alone. However, in comparison with the range of mean testis weights from all males examined (253-13,600 g), there is a relatively narrow range of mean testis weight at puberty (1500-3030 g). The geometric mean of the mean testis weights from the 11 males at puberty (shown in Fig. 1) is 1982 g. Only two immature males of the 101 shown had mean testis weights exceeding 2000 g (2122 and 2408 g respectively), while only one otherwise normal male having a mean testis weight below 2000 g (actual weight 1862 g) was post-pubertal.

In samples of vas deferens fluid from 51 males (see Table 8), sperms were found in only one where the mean testis weight was below 2000 g (actual mean weight 1830 g) and here the sperms were exceedingly rare. On the other hand sperms were present in all vas deferens samples from males whose mean testis weights exceeded 2000 g.

From the above considerations, the mean testis weight at puberty of humpback whales from the Western Australian coast is very close to 2000 g. This fact affords a rapid and relatively reliable means of distinguishing sexually immature males.

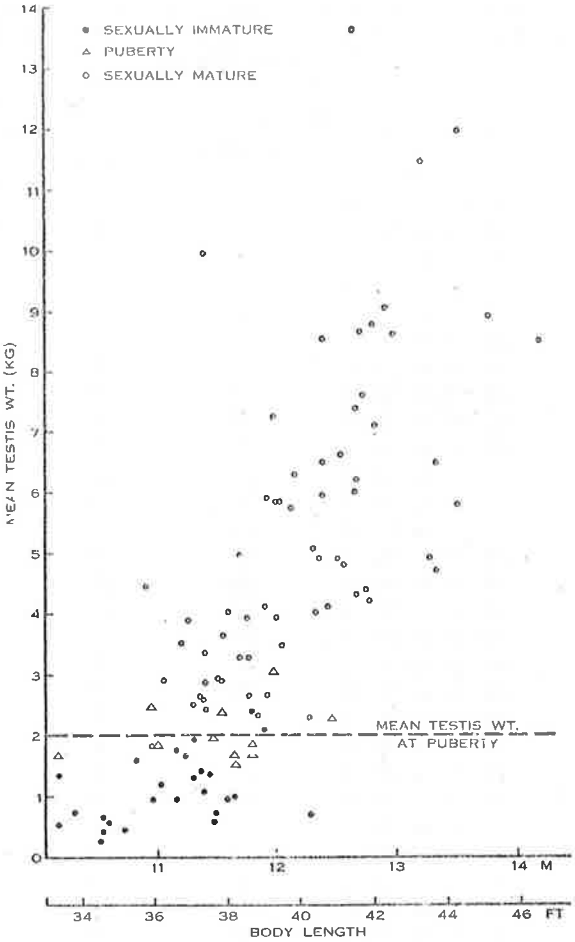

Fig. 1.—Testis weights (means of pairs) and body lengths of males whose testes were examined histologically.

(*b*) *Testis Weight*

Using the mean testis weight of 2000 g at puberty, the proportions of immature males in each 6-in. grouping of body length can be determined. Such a division on a basis of testis weight is shown in Table 1 for 609 males whose testes were weighed. The percentages of immature males in each 6-in. grouping of body length are shown in Figure 2. The curve in this figure indicates that at a length of 36 ft 9 in., 50 per cent. of male humpbacks would be sexually immature and 50 per cent. would have reached or passed puberty. This may be considered as the average length at puberty of male humpback whales.

TABLE 1

SEXUALLY IMMATURE MALES IN 6-IN. BODY LENGTH GROUPS, USING MEAN TESTES WT. OF 2000 G AS CRITERION OF PUBERTY

Body Length	Measurements Taken	Immature	
		Number	Per Cent.
ft in. ft in.			
30 0 to 30 5	1	1	100
30 6 to 30 11	—	—	—
31 0 to 31 5	1	1	100
31 6 to 31 11	1	1	100
32 0 to 32 5	—	—	—
32 6 to 32 11	1	1	100
33 0 to 33 5	7	7	100
33 6 to 33 11	7	7	100
34 0 to 34 5	3	3	100
34 6 to 34 11	11	11	100
35 0 to 35 5	10	9	90.0
35 6 to 35 11	15	10	66.7
36 0 to 36 5	11	8	72.7
36 6 to 36 11	22	10	45.5
37 0 to 37 5	24	10	41.7
37 6 to 37 11	29	7	24.1
38 0 to 38 5	31	8	25.8
38 6 to 38 11	42	3	7.1
39 0 to 39 5	54	1	1.9
39 6 to 39 11	44	0	0
40 0 to 40 5	46	2	4.3
40 6 to 40 11	49	0	0
41 0 to 41 5	47	0	0
41 6 to 41 11	40	0	0
42 0 to 42 5	42	0	0
42 6 to 42 11	24	0	0
43 0 to 43 5	16	0	0
43 6 to 43 11	12	0	0
44 0 to 44 5	7	0	0
44 6 to 44 11	6	0	0
45 0 to 45 5	2	0	0
45 6 to 45 11	2	0	0
46 0 to 46 5	1	0	0

Some confirmatory evidence of this length at puberty is adduced from Table 5, and from Figure 4, where the geometric means from the mean testis weights in 6-in. groupings of body length are shown. The geometric means from all length groups below 36 ft 6 in. are less than 2000 g, but those for all groups above this length exceed 2000 g.

(c) *Length of Penis*

Mackintosh and Wheeler (1929) suggested that in blue and fin whales the "size of the penis may be a useful means of deciding at a glance whether a whale is sexually mature or not, for this organ undergoes considerable growth at maturity". In the routine examination of hump-

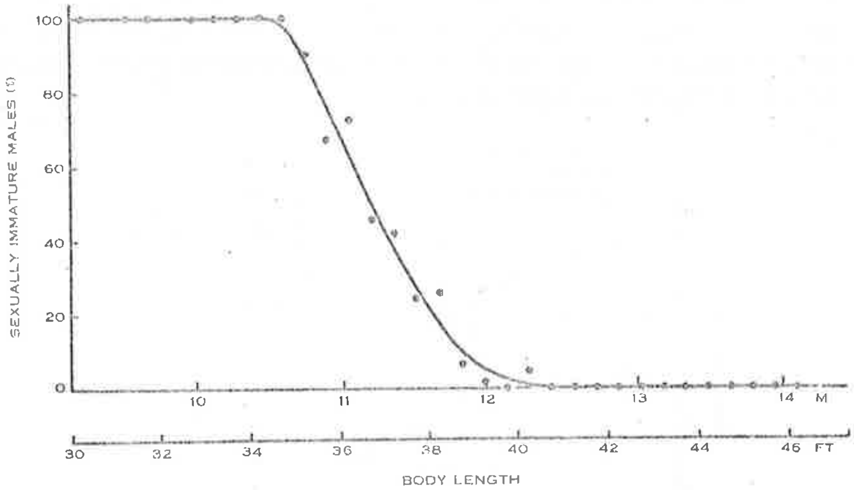

Fig. 2.—Proportions of sexually immature males in 6-in. groups of body length, using the mean testis weight of 2 kg as criterion of puberty.

TABLE 2

PENIS LENGTHS FROM MALES WHOSE TESTES WERE HISTOLOGICALLY EXAMINED

Immature		Puberty		Mature					
Body Length (ft)	Penis Length (ft)	Body Length (ft)	Penis Length (ft)	Body Length (ft)	Penis Length (ft)	Body Length (ft)	Penis Length (ft)	Body Length (ft)	Penis Length (ft)
33.33	2.92	33.33	3.58	35.75	4.33	39.08	3.92	41.50	4.58
33.75	1.67	35.92	4.00	35.92	4.42	39.08	4.50	41.50	5.17
34.58	3.67	36.08	2.75	36.25	4.75	39.25	4.25	41.50	5.25
36.17	3.58	37.58	4.17	36.75	3.75	39.33	4.25	41.58	4.25
36.58	3.25	38.17	4.08	36.92	3.17	39.33	4.42	41.67	3.83
36.58	3.75	38.17	3.67	37.25	3.83	39.42	4.50	41.75	5.33
36.83	2.58	38.67	2.17	37.33	4.58	40.33	4.33	41.92	3.58
37.08	2.67	39.25	3.42	37.42	3.50	40.42	4.50	42.00	5.00
37.08	3.67	40.83	3.42	37.83	3.75	40.50	4.67	42.25	4.75
37.25	2.92			37.92	3.67	40.58	4.42	42.50	4.58
37.50	3.50			38.00	4.25	40.58	4.83	43.25	4.75
37.58	2.67			38.33	3.83	40.58	5.17	43.50	4.25
38.00	2.17			38.50	4.08	40.75	4.33	43.67	4.83
38.17	2.42			38.58	4.08	41.08	3.83	43.67	5.00
40.25	3.25			38.83	4.25	41.42	4.75	44.25	4.75
				39.00	4.67	41.42	4.83	45.08	5.25
Mean: 2.98		Mean: 3.48		Mean penis length of 48 males: 4.41 ft					

back whales on the Western Australian coast, the length of the penis was recorded whenever possible. The penis was usually extruded when the whale was killed, but sometimes had been removed by sharks while the body was being brought into the station. The penis length of the mature humpback males examined range from 3.2 to 6.2 ft, which is considerably lower than that of 4.1-8.2 ft recorded by Matthews (1938*a*) from the same species in South Atlantic regions.

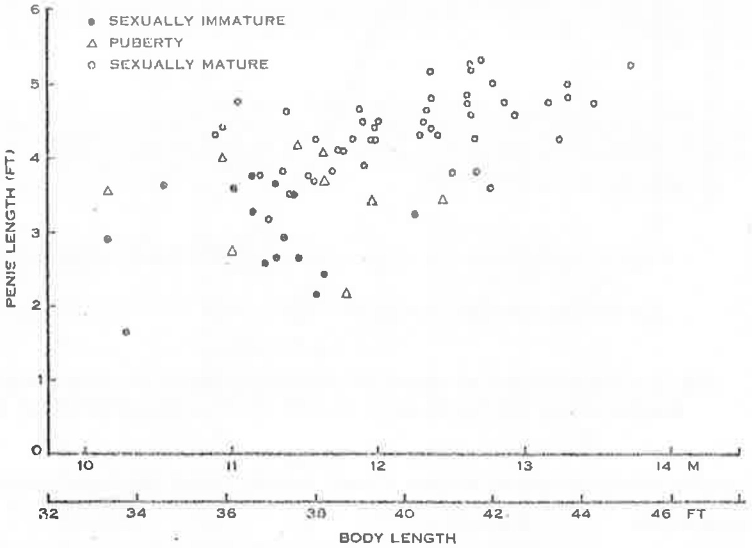

Fig. 3.—Lengths of penis and body lengths of males whose testes were examined histologically.

The penis lengths from 72 males, whose testes were examined histologically and so could be accurately classified as sexually immature, at puberty, or mature, are listed in Table 2 with body lengths. These records are plotted in Figure 3. There is some increase in penis length with increasing body length; this increase is slightly more rapid at puberty. Although males having a penis length of less than 3.5 ft (the mean length of the penis in males at puberty) were generally immature and those having a penis length exceeding 3.5 ft generally mature, a classification by means of penis length alone is not as reliable as that using a mean testis weight of 2000 g as an index of puberty.

It was found that the penis was often fully retracted (or sometimes only partially extruded) in immature males, while in almost all mature males it was fully extruded by the time the whale was hauled on to the flensing deck.

IV. Physical Maturity

Of 567 male humpback whales from the Western Australian coast where epiphyses were examined, 479 (83.5 per cent.) showed no epiphysial fusion, 80 (14.1 per cent.) were approaching physical maturity, while only 8 (1.4 per cent.) had attained physical maturity. The distribution of the body lengths of these males is shown in Table 3. The smallest male approaching physical maturity was 38 ft 5 in. in length, having epiphysial fusion up to the fifth lumbar vertebra, but this fusion may have been abnormal as there was a massive area of bone beneath the sixth and seventh lumbar vertebrae in this whale. The next males approaching maturity were two 38 ft 10 in. in length. On the other hand males of up to 46 ft 5 in. were found with no signs of epiphysial fusion. Total lengths and mean testis weights of males approaching, and at, full physical maturity are listed in Appendix I. These are summarized in Table 4.

TABLE 3

EPIPHYSIAL FUSION IN MALE HUMPBACK WHALES

Body Length	Total Examined	No Epiphysial Fusion		Fusion Begun		Full Fusion	
		No.	%	No.	%	No.	%
ft in. ft. in.							
Under 33 0	4	4	100				
33 0 to 33 5	7	7	100				
33 6 to 33 11	7	7	100				
34 0 to 34 5	3	3	100				
34 6 to 34 11	11	11	100				
35 0 to 35 5	10	10	100				
35 6 to 35 11	14	14	100				
36 0 to 36 5	11	11	100				
36 6 to 36 11	22	22	100				
37 0 to 37 5	24	24	100				
37 6 to 37 11	29	29	100				
38 0 to 38 5	25	24	96.0	1	4.0		
38 6 to 38 11	36	34	94.4	2	5.6		
39 0 to 39 5	46	45	97.8	1	2.2		
39 6 to 39 11	42	38	90.5	3	7.1	1	2.4
40 0 to 40 5	41	32	78.0	9	22.0		
40 6 to 40 11	45	38	84.4	7	15 6		
41 0 to 41 5	44	34	77.2	9	20.5	1	2.3
41 6 to 41 11	40	30	75.0	10	25.0		
42 0 to 42 5	38	25	65.7	11	29.0	2	5.3
42 6 to 42 11	24	15	62.5	9	37.5		
43 0 to 43 5	14	10	71.4	4	28.6		
43 6 to 43 11	12	6	50.0	5	41.7	1	8.3
44 0 to 44 5	7	3	42.9	4	57.1		
44 6 to 44 11	6	0	0.0	4	66.7	2	33.0
45 0 to 45 5	2	2	100				
45 6 to 45 11	2	0	0.0	1	50.0	1	50.0
46 0 to 46 5	1	1	100				
	567	479	84.5	80	14.1	8	1.4

The mean length at physical maturity is slightly above that at the onset of epiphysial fusion, but the fiducial limits for the former are wide.

TABLE 4

BODY LENGTH AND MEAN TESTIS WT. IN MALES NEAR AND AT PHYSICAL MATURITY

Stage of Development	Body Length (ft)				Mean Testis Wt. (g)		
	Min.	Max.	Mean	5% Fiducial Limits	Min.	Max.	Geom. Mean
Approaching maturity (80 males)	38.42	45.83	41.90	±0.35	2863	13,600	6352
At maturity (8 males)	39.83	45.50	42.97	±1.59	3660	11,230	6491

Although it is to be expected that the mean length at full physical maturity should be greater than that of those approaching physical maturity, a comparison of these two groups by means of the t test was inconclusive, as $t = 1.8$ on 86 degrees of freedom.

V. CHANGES DURING THE LIFE CYCLE

(*a*) *Testis Weight*

Table 5 shows the ranges and geometric means of the mean testis weights from 620 males in 6-in. body length groups and for several in the late foetal stages. Over the limited length range (12 ft 9 in. to 15 ft 5 in.) of the late foetuses whose testes were weighed, there is no evidence of any direct relationship between foetal body length and mean testis weight. Omitting these foetal records, the geometric means given in Table 5 are shown against body length in Figure 4. Included in Figure 4 are the geometric means of testis weights of humpback whales from the Antarctic reported by Omura (1953). These are considered in Section VI(*a*).

The testis weights from Western Australian coast humpback whales in Figure 4 show only a slight increase with body length during the greater part of the immature phase. Shortly before puberty, testis weight begins increasing more rapidly and continues to rise sharply for some time after this stage is reached. In larger (relatively older) mature males the variation in mean testis weight is considerable but independent of body length.

Figure 4 shows a group of very similar geometric means of testis weights between body lengths of 39 ft 6 in. and 41 ft 6 in. This break in an otherwise relatively regular rise in testis weight, occurring as it does in groups where the records are of high frequency (see Table 5), would be expected to be of some biological significance. Possibly this represents a young class of sexually mature individuals. The geometric means of the last five groups from the Western Australian series cannot be usefully discussed, the records in each being of low frequency and high variability.

TABLE 5

MALE HUMPBACK WHALES: RANGES AND GEOMETRIC MEANS OF MEAN TESTIS WEIGHTS

Body Length	Measurements Taken	Range (g)	Geom. Mean (g)
ft in. ft in.			
12 9 to 15 5*	11	22-56	36.3
30 0 to 30 5	1	—	253
30 6 to 30 11	0	—	—
31 0 to 31 5	1	—	291
31 6 to 31 11	1	—	262
32 0 to 32 5	0	—	—
32 6 to 32 11	1	—	553
33 0 to 33 5	7	365-1673	632
33 6 to 33 11	7	348-781	579
34 0 to 34 5	3	338-842	523
34 6 to 34 11	11	260-1695	604
35 0 to 35 5	10	480-2820	836
35 6 to 35 11	15	542-4455	1486
36 0 to 36 5	11	540-4512	1572
36 6 to 36 11	22	420-6520	2164
37 0 to 37 5	24	593-9045	2222
37 6 to 37 11	29	606-9945	2951
38 0 to 38 5	31	667-8575	3234
38 6 to 38 11	42	1095-8272	3982
39 0 to 39 5	54	1990-8925	4516
39 6 to 39 11	44	2275-10,850	5432
40 0 to 40 5	46	704-11,260	5698
40 6 to 40 11	49	2250-9770	5672
41 0 to 41 5	47	2315-13,600†	5609
41 6 to 41 11	40	2700-11,190‡	6350
42 0 to 42 5	42	3660-12,200	6597
42 6 to 42 11	24	4055-11,442	6533
43 0 to 43 5	16	2640-12,260	6713
43 6 to 43 11	12	4710-10,900	6765
44 0 to 44 5	7	5465-11,968	7812
44 6 to 44 11	6	4020-11,230	7843
45 0 to 45 5	2	8880-9995	9421
45 6 to 45 11	2	5095-8155	6446
46 0 to 46 5	1	—	8030

* Late foetal males.

† One record of 1018 g omitted as testes were definitely abnormal.

‡ One record of 673 g omitted as testes were definitely abnormal.

Males at physical maturity have mean testis weights very similar to males at the onset of epiphysial fusion, the geometric means being 6491 and 6352 g respectively (Table 4). These lie close to the geometric means of testis weights from corresponding groups of body length shown in Figure 4, in the region where testis weight is no longer rapidly increasing with body length. In Figure 5 the mean testis weight is shown against body length in each of 80 males approaching physical maturity. The range of testis weight is wide and there is no direct relationship between testis weight and body length in these males.

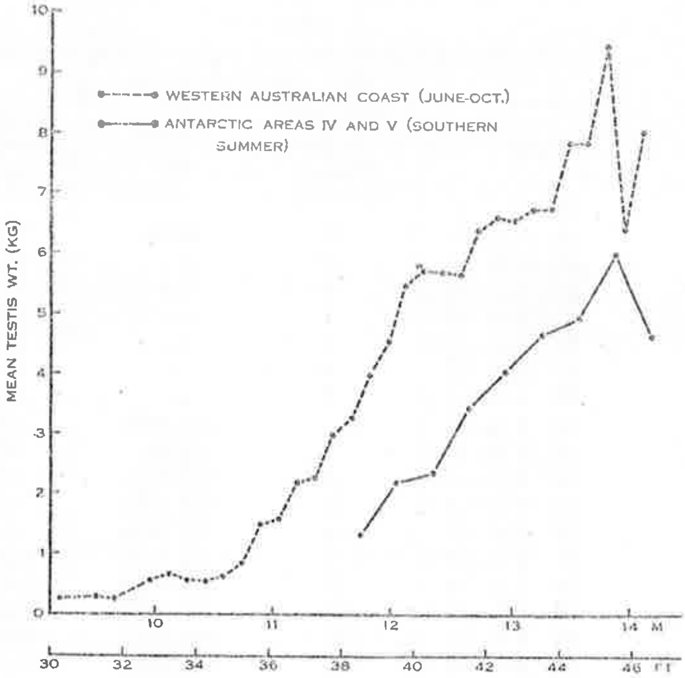

Fig. 4.—Geometric means of mean testis weights in 6-in. groups of body length. Japanese (Antarctic) records in 1-ft groups.

Table 6

MINIMA, MAXIMA, AND MEANS OF MEAN TUBULE DIAMETERS FROM TESTES IN FOUR STAGES OF LIFE CYCLE

Stage	Number Examined	Mean Dia. of Testis Tubules		
		Min. (μ)	Max. (μ)	Mean (μ)
Foetal	5	58	81	66
Immature	26	59	112	79
Puberty	11	87	121	103
Mature	65	108	199	155

(b) *Changes in Diameter of Testis Tubules*

The mean tubule diameters of 107 male humpback whales are shown against body length in Figure 6, each male being classified as late foetal, immature, at puberty, or mature. Table 6 shows the ranges and means of these mean tubule diameters for the four stages.

Figure 6 shows that there is very little increase in diameter of testis tubules from the late foetal stage until puberty. Yet there is an increase in mean testis weight from a mean of 36.3 g (in the late foetal stage) to nearly 2000 g during this period (see Table 5). During this phase of testis growth the testis tubules must increase considerably in length, but very little in diameter. In this regard it was noticed that there were more tubules crowded closer together in a given area of sections of immature testes than those of late foetal testes (Plate 1, Figs. 2 and 1 respectively).

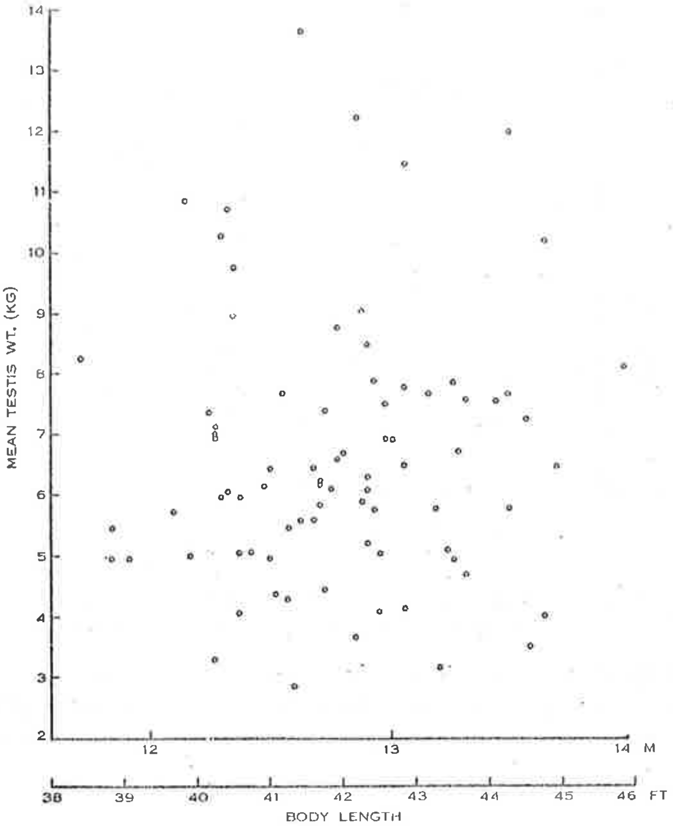

Fig. 5.—Mean testis weights and body lengths of males approaching physical maturity.

Two other differences between foetal and immature testes were noted. Firstly, sections of foetal testes showed more blood vessels (packed with erythrocytes) than those at any other stage. Secondly, in most instances the contents of the tubules of immature testes were shrunk away from the interstitium (see Plate 1, Fig. 2). This condition did not appear to be related to post-mortem changes nor to the methods of fixation, as it did not appear in foetal or mature material treated in the same way. At puberty the contents of the larger tubules with lumina were not shrunken from the wall (Plate 1, Fig. 3), while in other areas of the same material the smaller, inactive tubules were frequently of the same shrunken appearance as found in immature testes.

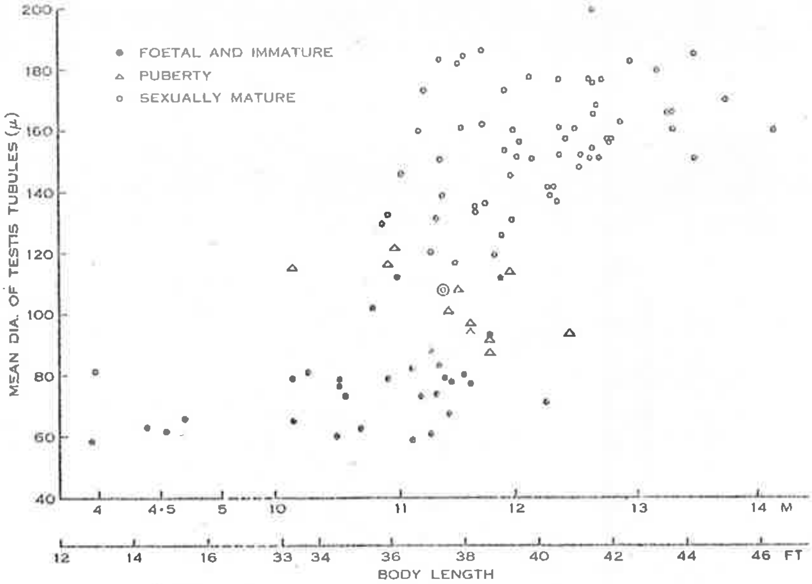

Fig. 6.—Mean diameter of testis tubules and body length of males at late foetal, immature, puberty, and mature phases.

Figure 6 demonstrates that at puberty there is a rapid increase in diameter of testis tubules. This change does not take place simultaneously in all tubules of a testis, some tubules enlarging suddenly, a lumen appearing with occasional dividing spermatocytes, while other tubules are still closed showing no signs of activity. An example of this type of activity is shown in Plate 1, Figure 3. Twenty measurements have been made both of inactive closed tubules and of open tubules in which spermato-

Table 7

Diameters of Closed and Open Tubules in the Testes of Four Males at Puberty

Dia. of Closed Tubules			Dia. of Open Tubules		
Min. (μ)	Max. (μ)	Mean (μ)	Min. (μ)	Max. (μ)	Mean (μ)
55	99	72	89	142	106
62	95	78	89	139	106
52	105	80	95	142	114
71	108	87	95	123	109

genesis was commencing in the testes of four of these males at puberty. These are summarized in Table 7.

Table 6 shows the mean tubule diameter from 11 males at puberty to be 103 μ, which is in fair agreement with the mean tubule diameters of the open tubules of the above four males where maturation of a few tubules had begun.

Figure 6 shows that the seminiferous tubules continue to increase rapidly in diameter for a period immediately after puberty, but that later there is little further increase in tubule diameter.

(c) *Spermatozoa in Testis Tubules*

The numbers of sperms in sections of testis tubules (cut at a thickness of 7 μ) vary to some extent, not only along one tubule but also between different tubules. However, the average number of sperms in 20 tubule sections selected at random does serve as an index of the relative activity of spermatogenesis in the testis.

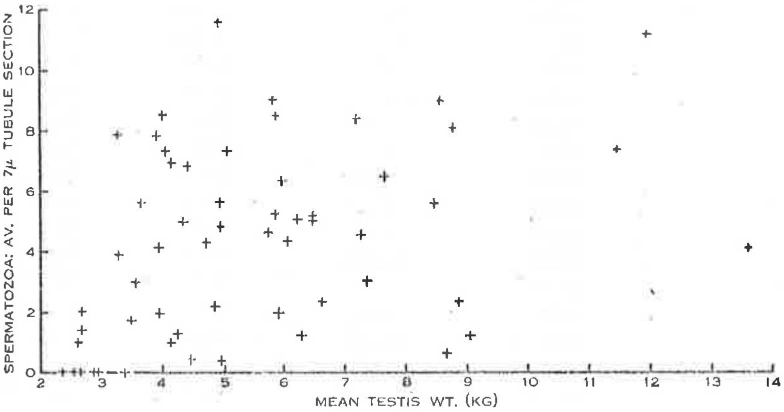

Fig. 7.—Average number of spermatozoa per testis tubule section (7 μ thick) and mean weight of testes.

Figure 7 gives the results of such sperm counts, the average numbers of sperms per tubule section (7 μ thick) being plotted against the corresponding mean testis weights. Numbers of sperms per tubule section are always relatively low in humpback whales. Mackintosh and Wheeler (1929) commented upon the paucity of sperms in the testes of blue and fin whales at all times of the year.

Figure 7 shows that shortly after puberty, when the mean testis weight is from 2000 to 3000 g, there are very few sperms in the testes. Sperms are more common in whales whose mean testis weights exceed 3000 g, but their number does not increase with testis weight.

Variation in the numbers of sperms in the testes during the months of June to October are discussed in Section VI (*c*).

(d) *Spermatozoa in Vas Deferens Fluid*

(i) *Density.*—The vasa deferentia in mature male humpback whales taken off the Western Australian coast in winter are generally swollen with seminal fluid, sometimes so much that some portions appear slightly bulbous. The results of the sperm counts upon vas deferens fluid from 50 male humpback whales are listed in Table 8, which includes the mean testis weight and total length of each whale and the date upon which it was killed. Sperms were present in the vas deferens fluid of only one

TABLE 8

SPERM COUNTS ON VAS DEFERENS FLUID

Mean Testis Wt. (g)	Sperm Density (10^6/c.c.)	Body Length (ft)	Date Killed
681	0	34.58	Sept. 3
704	0	40.33	Aug. 29
949	0	38.00	Sept. 3
1015	0	38.17	Aug. 5
1099	0	37.33	Aug. 29
1413	0	37.25	Aug. 14
1673	0	33.33	Aug. 27
1682	0	38.67	Aug. 5
1830	<0.250	36.08	Sept. 17
1846	0	38.67	Aug. 5
2597	1.250	37.33	Aug. 9
2630	0.250	37.25	Aug. 4
2664	0.375	39.08	June 18
3648	31.000	37.92	Sept. 4
3925	7.500	38.50	July 5
3930	7.250	39.33	Aug. 13
4016	87.500	38.00	Aug. 11
4045	19.500	40.42	Aug. 13
4125	15.500	39.00	Aug. 29
4135	97.000	40.75	Aug. 31
4220	36.500	41.83	Aug. 9
4420	32.500	41.75	Sept. 10
4710	26.000	43.67	Sept. 24
4830	6.000	41.17	June 11
4918	49.000	41.00	Aug. 12
4943	26.750	40.50	Aug. 7
4950	17.500	38.33	July 30
4960	83.500	43.50	Sept. 5
5080	68.250	40.33	Aug. 7
5740	164.250	39.75	July 30
5810	59.250	44.25	Aug. 3
5860	29.250	39.42	Sept. 25
5865	72.750	39.33	Aug. 13
5900	156.750	39.08	Sept. 19
5965	171.250	40.58	Sept. 23
6015	48.150	41.50	July 4
6213	104.775	41.50	Aug. 22

TABLE 8 (*Continued*)

Mean Testis Wt. (g)	Sperm Density (10^6/c.c.)	Body Length (ft)	Date Killed
6290	4.500	39.83	July 4
6483	24.000	43.67	Sept. 2
6498	86.000	40.58	Aug. 11
6935	89.000	40.25	July 10
7160	94.500	42.00	Aug. 28
7268	130.500	39.25	Sept. 23
7632	66.250	41.67	July 30
8480	78.000	46.42	Aug. 11
8545	41.500	40.58	July 11
8780	21.250	41.92	Sept. 29
9060	21.250	42.25	Aug. 4
11,968	175.000	44.25	Sept. 4
13,600	22.000	41.42	Sept. 10

male with a mean testis weight of less than 2000 g, and in this specimen only one sperm was seen. On the other hand, sperms were present in the vas deferens fluid of all males having a mean testis weight exceeding 2000 g. This supports the evidence in Section III (*a*) that the mean testis weight at puberty is 2000 g. In Figure 8 the density of sperms in vas deferens fluid is plotted against the mean testis weight for the males in Table 8, excluding those sexually immature. In the lower testis weight groups the density of sperms increases with the mean testis weight.

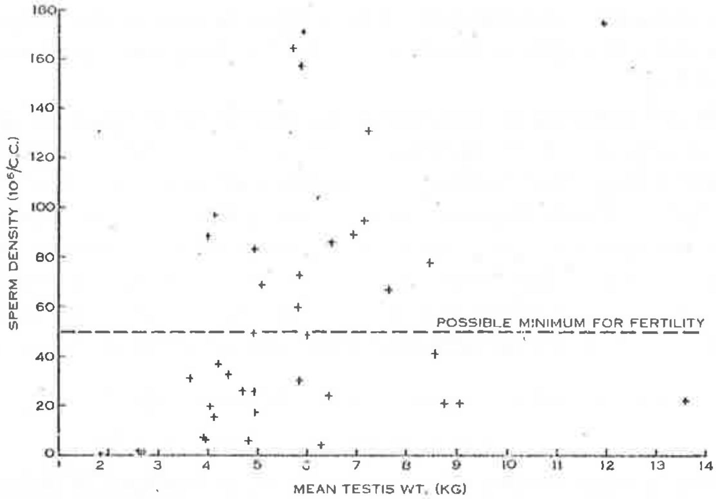

Fig. 8.—Density of sperms in vas deferens fluid and mean testis weight.

Neither the degree of dilution of fluid in the vas deferens on ejaculation, nor the minimum density of sperms required for copulation to succeed in conception is known in whales. However, if the density of 50×10^6 sperms/c.c. used by Harvey and Jackson (1945) as a criterion of fertility in human males is applied to the sperm counts in vas deferens fluid from humpback whales, most of those males having a mean testis weight of less than 5000 g would be classed as of low fertility, and the majority of those whose mean testis weight exceeded 5000 g would be (on a basis of sperm density alone) fertile. Some of the lower sperm densities in males of relatively high testis weight might be the result of copulation immediately prior to killing.

Very large numbers of epithelial cells were present in some samples of vas deferens fluid. These cells, roughly columnar and sometimes in small blocks, appeared to be degenerating, with little sign of nuclei even in the freshest material. Such cells appeared irregularly in seminal fluid with no apparent relationship to the presence or density of sperms.

(ii) *Morphology of Spermatozoa.*—Normal sperms from humpback whales are very similar morphologically to human sperms, having flattened oval-shaped heads 3-5 μ long. In total length they ranged from 32.2 to 64.4 μ with a mean length (from 50 measurements) of 52.5 μ. This may be compared with the total length of human sperms, given by Schafer (1949) as approximately 50 μ and by Maximow and Bloom (1948) as 61-62 μ. Sperm lengths have been recorded for two other species of Cetacea; Asdell (1946) quotes the sperms of the sperm whale as measuring 40.6 μ in length, and Retzius (1909) records that in the porpoise (*Phocaena communis*) the sperm head was 5.4-6.3 μ long and the total length of the sperm 73.8 μ.

In all samples of seminal fluid examined at least 80 per cent. of the sperms appeared to be normal, fulfilling the second criterion of Harvey and Jackson (1945) for fertility. In almost all samples a few abnormal forms were seen. These included the double, giant, and pin-head forms as well as double tail and thick neck types described by Harvey and Jackson in human semen. Such forms were included in the sperm counts listed above. Abnormal sperms did not appear to be present in different proportions in vas deferens fluids of low and high sperm density respectively.

VI. Evidence of Seasonal Activity in Mature Testes

(*a*) *Changes in Testis Weight*

For a comparison of testis weights in humpback whales at different periods of the year, individuals of the same age group should be used. While the precise ages of these males are not known, those approaching physical maturity (epiphysial fusion begun but not complete throughout the vertebral column) should be of approximately the same age. It is shown in Section V(*a*) that in males approaching physical maturity the mean testis weight is no longer increasing with body length. In Figure 9 the mean testis weights of 80 males approaching physical maturity are plotted against the dates upon which these whales were killed. Although few records are available in June, there is no evidence of any change in testis weight of these males between June and early October.

Omura (1953) recorded testis weights from humpback whales in the Antarctic areas IV and V. The geometric means given by him for 1-ft body length groups are shown in Figure 4 with the geometric means for 6-in. body length groups of males from the Western Australian coast. This shows that for males of corresponding body lengths, the testis weights from Antarctic individuals were always markedly less (24-64 per cent.) than those from Western Australian coast males.

On the evidence of testis weights from the Antarctic and from the Western Australian coast there is a seasonal variation in testis weights of mature humpback whales, with low testis weights in the Antarctic during the summer and much higher weights off the Western Australian coast during the winter and spring.

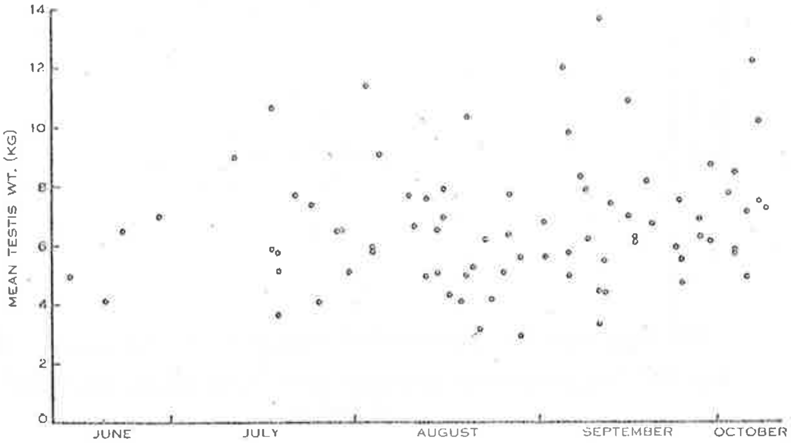

Fig. 9.—Mean testis weights of males approaching physical maturity and dates of killing.

(b) *Diameter of Testis Tubules*

In Figure 10 the mean diameters of the testis tubules from 64 mature humpback whales are shown together with the dates upon which the whales were taken. Smaller tubule diameters were more frequent in the testes of males taken in August than in other months. However, the majority of these lower mean tubule diameters were from younger males of shorter body length and lower mean testis weight taken soon after puberty, so that (as shown in Section V(*b*)) their testis tubules were still in a period of rapid increase in diameter. Disregarding the younger males with low mean tubule diameters which were of more frequent occurrence in August, Figure 10 gives no evidence of a cyclic variation in diameter of the testis tubules of sexually mature male humpback whales from June to early October.

(c) *Spermatozoa in Testis Tubules*

In Section V(c) it was shown that very few sperms were seen in the testis tubules of males having mean testis weights less than 3000 g, but that the greater numbers of sperms present when the mean testis weight exceeded 3000 g were independent of increasing mean testis weight.

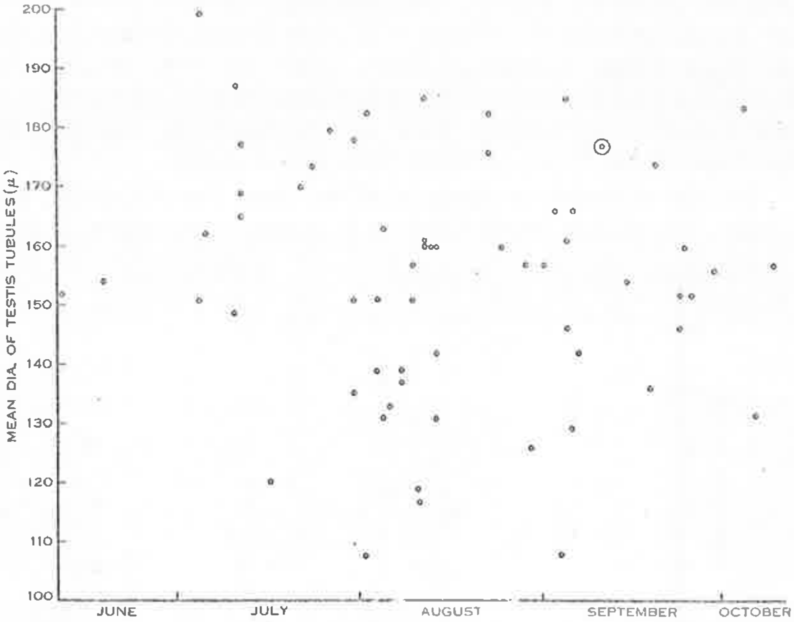

Fig. 10.—Mean diameters of testis tubules from mature males and dates of killing.

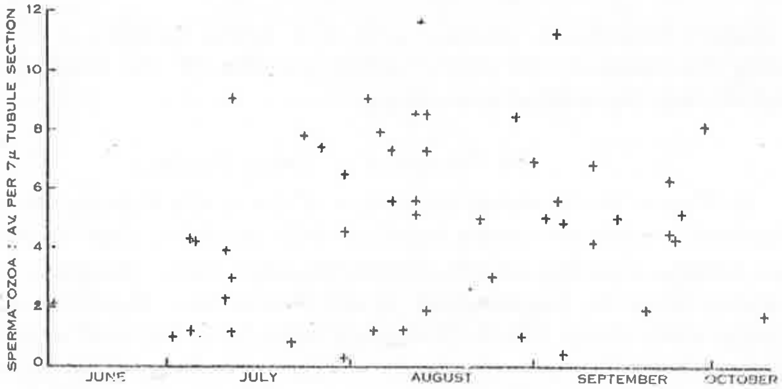

Fig. 11.—Average number of spermatozoa per testis tubule section (7 μ thick) of mature males whose mean testis weights exceeded 3 kg, and dates of killing.

In Figure 11 the average number of sperms per tubule section is shown against the date of killing for males whose mean testis weight exceeded 3000 g. Over the period when whales were taken (June to October), fewer sperms were present in the testes of mature males taken early in the season. Sperms were generally more plentiful in the testes of those taken in late July and August and, although still common in the testes of September killings, appeared to be a little below the peak of late July and August. Similar counts of sperms from the testes of male humpback whales taken in Antarctic regions would no doubt strengthen this evidence of a seasonal cycle of spermatogenetic activity, as Matthews (1937) found no sperms in the testes of four mature male humpback whales taken at South Georgia in December, January, and March.

(*d*) *Density of Sperms in Vas Deferens Fluid*

In Section V(*d*) it was shown that the density of sperms in vas deferens fluid tended to increase with mean testis weight up to 5000 g, after which there was no apparent relationship between sperm density and mean testis weight. In Figure 12 the densities of sperms in the vas deferens fluid of males whose mean testis weight exceeded 5000 g are shown with the times of killing. The records are insufficient to allow definite conclusions to be drawn but, considering the density of 50×10^6 sperms/c.c. tentatively used in Section V(*d*) as a criterion of fertility, the majority of those taken in early July would have been of low fertility, while from late July to September the greater proportion would have been fertile males (on this basis of sperm density alone).

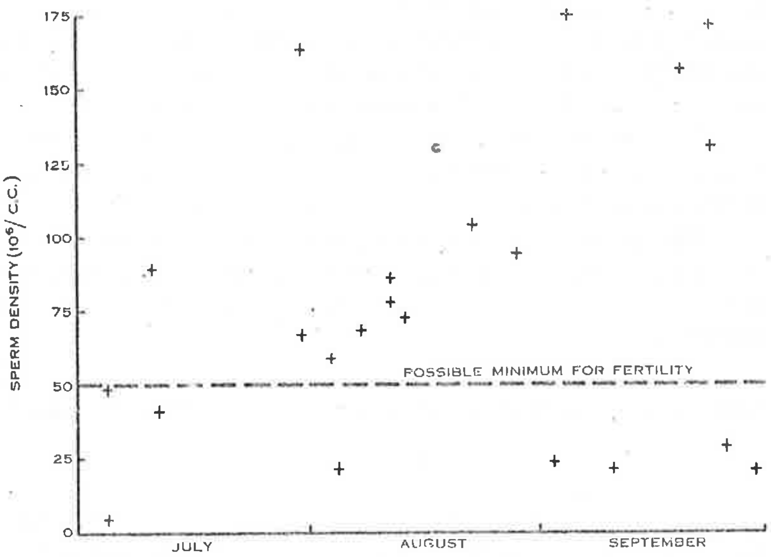

Fig. 12.—Density of sperms in vas deferens fluid of mature males whose mean testis weights exceeded 5 kg, and dates of killing.

In two successive years it was noticed while collecting vas deferens fluid that there was very often less fluid available from mature males taken in June and early July. Thus it is possible, by reason of low volume of semen and lower density of sperms, that mature male humpbacks are of lower fertility until late July. This conclusion is supported by the lower sperm counts on testis tubule sections in June and early July. Densities of vas deferens fluid taken from mature males in Antarctic areas would be of great value in any consideration of the seasonal cycle in male humpback whales.

VII. DISCUSSION

(a) *Puberty*

From histological examination of testes and analysis of mean testis weights it has been found that the average body length of male humpback whales from the Western Australian coast at puberty is 36 ft 9 in., with an extreme range from 33 ft 4 in. to 40 ft 10 in. Because of the relatively wide range in body length of individual males at this stage, body length alone is not sufficient to enable any one specimen within this range to be accurately diagnosed as having reached puberty. However, the average length of 36 ft 9 in. is important in catch analyses, offering a relatively reliable means of determining the proportion of sexually immature males in the yearly catch.

The mean testis weight of these males at puberty is 2000 g, so that the testis weight is a simple field guide (in the absence of histological methods) to the sexual conditions of individual males taken off Western Australia.

In this species puberty is generally reached at the end of the second year of life, but may sometimes be delayed until the end of the third year.

(b) *Sexual Maturity*

Following puberty there is a period of rapid increase in testis weight and diameter of seminiferous tubules. During this phase few sperms are present in the seminiferous tubules and the concentrations of sperms in vas deferens fluid are generally low. Such young males would be of suboptimal fertility. This indicates that sexual maturity (when full reproductive powers have been reached) is not attained until a further period, probably a year, after puberty.

(c) *Penis*

The size of the penis is not generally recorded in work on other groups of mammals, but Mackintosh and Wheeler (1929) noted that in blue and fin whales the penis increases considerably in size at "sexual maturity". In humpback whales the length of the penis increases with body length, with a more rapid increase at puberty. The mean length of the penis at puberty is 3.5 ft; the majority of males having a penis length of less than 3.5 ft are sexually immature, but the length of the penis alone is not a reliable guide. In the mature males examined the length of the penis ranged from 3.2 to 6.2 ft, which is considerably lower than that of 4.1-8.2 ft recorded by Matthews (1937) for the same species in South Atlantic regions.

(d) *Testis Weight*

After a slow rise during immaturity (when body length is fast increasing), testis weight begins increasing more rapidly shortly before puberty and continues to rise sharply for a period after this stage is reached. Later in life testis weights vary widely in individual males and show no relationship to body length. Similar increases in testis weights are recorded by Brody (1945) in man, by Robson (1949) in the bull, and by Jonsgard (1951) in the minke whale. Mackintosh and Wheeler (1929) obtained similar results with the volume of the testes of blue and fin whales.

TABLE 9

MEAN DIAMETERS OF TESTIS TUBULES FROM VARIOUS SEXUALLY MATURE MAMMALS

Species	Author	Number Examined	Mean Dia. of Testis Tubules Min. (μ)	Max. (μ)	Mean* (μ)
Polar bear	Knepp (1939)	1	—	—	105.8
Virginia deer	Knepp (1939)	1	—	—	139.4
Wallaroo	Knepp (1939)	1	—	—	141.1
Mouflon	Knepp (1939)	1	—	—	149.5
Humpback whale	Chittleborough†	65	108	199	155
Grey squirrel	Knepp (1939)	1	—	—	169.7
Cottontail rabbit	Knepp (1939)	1	—	—	173.9
Punjab wild sheep	Knepp (1939)	1	—	—	176.4
Man	Bascom and Osterud (1925)	1	—	—	183
Belgian hare	Bascom and Osterud (1925)	1	—	—	184
Albino mouse	Bascom and Osterud (1925)	3	191	201	194
Sheep	Bascom and Osterud (1925)	1	—	—	211
Dog	Bascom and Osterud (1925)	2	207	217	212
Pig	Bascom and Osterud (1925)	2	223	225	224
Guinea-pig	Bascom and Osterud (1925)	7	198	244	226
Bull	Bascom and Osterud (1925)	4	198	238	228
Albino rat	Bascom and Osterud (1925)	5	242	265	253

* Mean from all males examined.

† Present paper (Table 6).

(e) *Testis Tubules*

The mean diameter of the seminiferous tubules increases very little from the late foetal stage until shortly before puberty. At puberty some tubules begin enlarging, with development of a lumen and spermatocytes, before others show any change from the immature condition. The mean tubule diameter at puberty is 105 μ. Tubules continue to increase in diameter for a period after puberty (Fig. 6), later becoming more constant when males are sexually mature. Tubule diameters vary very little in different parts of a mature testis; for example, the mean tubule diameters from two samples of tissue from one testis were 161 and 159 μ.

Table 9 lists the mean diameters of seminiferous tubules from mature individuals of various mammals. Although the humpback whale has the largest testes of this series, the tubule diameter is relatively low. The size of the spermatozoa of the humpback whale is also within the range found in other species of mammals, the average length of sperms in this species being 52.5 μ.

While examining seminiferous tubules in sections of humpback testes it was noted that blindly ending branches were more common than in the testes of other mammals, for example, the rabbit (Huber and Curtis 1913) and man (Johnson 1934). In the humpback whale these branches were more common towards the surface of the testes, a single tubule leading to two short, blindly ending tubules of similar diameters to the original tubule. As such branching of seminiferous tubules is generally considered to be rare in mammals, this may be worthy of further investigation in the humpback and other species of Cetacea.

(*f*) *Sperm Concentrations in Vas Deferens Fluid*

Since it is not possible to obtain samples of ejaculatory fluid from whales, the vas deferens fluid has been examined. The concentrations of sperms in vas deferens fluid cannot be easily compared with those from ejaculatory fluid of other mammals, since in all species the sperms are diluted (sometimes greatly) on ejaculation by the secretions of accessory glands. The densities of sperms in vas deferens fluid from sexually mature male humpback whales taken off the Western Australian coast during July, August, and September ranged from 4×10^6 to 175×10^6 per c.c. with a mean value of 78.6×10^6 per c.c. This appears to be low for vas deferens fluid in comparison with the concentrations of sperms in ejaculatory fluid from the bull, ram, stallion, and boar (Perry 1952) and man (Harvey and Jackson 1945). However, in the Cetacea it is probable that there is less dilution of sperms on ejaculation, since vesiculae seminales and Cowper's glands have not been found in whales, though the prostate glands are present (Meek 1918, Ommanney 1932). Ommanney found that in the Cetacea the glands of the prostate are of primitive form, similar in arrangement to those in marsupials.

(*g*) *Physical Maturity*

The mean length of the physically mature males examined is 42.97 ± 1.57 ft and that of those approaching physical maturity (epiphysial fusion begun but not extending throughout the vertebral column) is 41.90 ± 0.35 ft, so that there is little further increase in body length once epiphysial fusion begins. The largest male whose epiphyses were examined was 46.42 ft in length and in this male epiphysial fusion had not commenced. No evidence has been found of any decline in testis weight or spermatogenetic activity in physically mature males.

Only 8 (1.4 per cent.) of 567 male humpback whales whose epiphyses were examined had reached full physical maturity. (Similarly, only 6 (1.8 per cent.) of 327 females were physically mature.) This very low proportion of physically mature males in a random sample of the catches off Western Australia from 1951 to 1953 might be due to one or more of the following causes: (i) such males might migrate farther offshore or not all move from Antarctic waters; (ii) physical maturity might be reached relatively late in life in humpback whales; (iii) owing to previous heavy fishing with a strong selectivity towards larger individuals, most of the physically mature animals may have been removed from the stock. At present there is no evidence to suggest that physically mature humpback whales differ from other individuals in their migratory habits. While it is considered likely that physical maturity is attained relatively late in life in this species, it would be of interest to compare the proportion of physically mature individuals in the Western Australian group with that in a less heavily fished population of humpback whales. This will be possible when the research begun by the Division of Fisheries, C.S.I.R.O., upon the humpback whales from the eastern Australian coast is further advanced.

(*h*) *Seasonal Cycle in Sexually Mature Males*

A cyclic variation in the weight or volume of testes from mature animals is generally accepted as sufficient to demonstrate seasonal sexual activity in males. Such a male sexual cycle has been demonstrated in a variety of mammals: moles (Asdell 1946), the hedgehog (Robson 1949), the water shrew (Price 1953), bats (Asdell 1946), deer (Wislocki 1949), the snowshoe hare, marmot, wood rat, prairie dog, and squirrels (Asdell 1946), the woodchuck (Robson 1949), the cottontail rabbit, ferret, stoat, and Siberian sable (Asdell 1946), and the fox (Rowlands and Parkes 1935). In the Cetacea, Meek (1918) has presented some evidence that the testes of the porpoise (*Phocaena communis*) undergo great development in the summer (northern hemisphere), the breeding season being in July and August.

In those species of whales which annually make long migrations from circumpolar feeding grounds to temperate and subtropical areas where the females undergo parturition and oestrus (see Mackintosh and Wheeler (1929) for blue and fin whales, Matthews (1937) and Chittleborough (1954) for humpback whales), a seasonal sexual cycle might also be expected in the males. Mackintosh and Wheeler were unable to demonstrate a seasonal change in testis volume from sexually mature blue and fin whales, but found sperms to be more plentiful in the testes of males taken off South Africa in May than in the testes of those taken in the Antarctic during summer months. With the humpback whale, Matthews found some sperms in the testes of three mature males taken off South Africa in July and August, but none in the testes of four mature males taken off South Georgia in December, January, and March. In the northern hemisphere, Engle (1927) found no sperms or spermatids in the testes of three male humpback whales at Trinidad, California, in August and from this suggested a seasonal cycle in the North Pacific with breeding occurring during the winter months.

In this investigation changes in testis weight, diameter of seminiferous tubules, numbers of sperms in testis tubule sections, and density of sperms in vas deferens fluid have been considered for evidence of a seasonal sexual cycle in male humpback whales. Using mean testis weights from males approaching physical maturity (approximately the same age), no regular variation in testis weight was found off the Western Australian coast during the months of June to October. However, testis weights recorded by Omura (1953) from males taken in the Antarctic in the summer were much lower than those from males of the same length taken off the Western Australian coast in winter (Fig. 4), indicating that a seasonal variation in testis weight does occur in sexually mature male humpback whales.

No evidence has been found of a cyclic variation in diameter of seminiferous tubules from mature males between June and October. Since testis weights are lower in summer individuals taken in Antarctic waters, the tubules might be of smaller diameter in this period, but no measurements are yet available. Cyclic variations in the size of the seminiferous tubules have been demonstrated in the ferret (Asdell 1946), but are better known in those species of birds (Watson 1919; Marshall 1949, 1950, 1951) in which the testes undergo great development during the breeding season.

Not only by the seasonal variation in testis weight, but also on the evidence of sperm counts in sections of seminiferous tubules between June and October (supported by the finding by Matthews (1937) of no sperms in the tubules of mature males in Antarctic waters during the summer) a seasonal cycle of testis activity can be postulated in mature male humpback whales. Spermatogenesis appears to be at a peak in late July and August, and though still active in September shows slightly less activity in this month. This agrees well with the ovulatory cycle in the female humpback whale, where it has been shown (Chittleborough 1954) that ovulation is of maximum frequency in late July, is still of frequent occurrence in August, and continues to occur in September to a lessened degree.

Variations in the concentrations of sperms in vas deferens fluid from sexually mature males taken off the Western Australian coast give some support to the evidence of an annual cycle of spermatogenetic activity.

However, since only the active part of the cycle can be studied here, counts of sperms in vas deferens fluid are required from males taken in Antarctic regions during summer months.

VIII. ACKNOWLEDGMENTS

The cooperation of the Norwest Whaling Company and the Australian Whaling Commission, enabling me to collect material at their respective shore stations at Point Cloates and Carnarvon, is gratefully acknowledged.

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EXPLANATION OF PLATE 1

Fig. 1.—Section of testis from a late foetal male humpback whale. Body length 14 ft 11 in. Average tubule diameter 62 μ. Capillaries filled with erythrocytes common. × 125.

Fig. 2.—Section of testis from a sexually immature male. Average tubule diameter 73 μ. Shrinkage of tubule contents after fixation as commonly found in immature humpback testes. × 125.

Fig. 3.—Section of testis from a male at puberty. Most tubules closed and contents shrunken from wall; average diameter 72 μ. Some tubules enlarging, with a lumen and few spermatocytes; average diameter 106 μ. × 125.

Fig. 4.—Section of testis from a sexually mature male taken during the breeding season. Average tubule diameter 160 μ. Spermatocytes, spermatids, and spermatozoa present. × 125.

APPENDIX I

MALE HUMPBACK WHALES NEAR AND AT PHYSICAL MATURITY

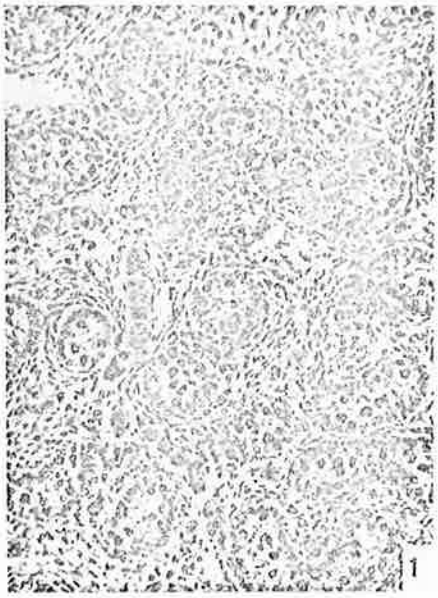
(*a*) Epiphysial Fusion Begun but not Complete

Body Length	Mean Testis Weight (g)	Point of Last Fusion	Body Length	Mean Testis Weight (g)	Point of Last Fusion	Body Length	Mean Testis Weight (g)	Point of Last Fusion
ft in.			ft in.			ft in.		
38 5	8270	5 Lumbar	41 3	4290	8 Thoracic	42 6	5035	3 Lumbar
38 10	4960	11 Lumbar	41 3	5460	4 Lumbar	42 7	6925	11 Lumbar
38 10	5465	7 Lumbar	41 4	2863	9 Lumbar	42 7	7505	10 Lumbar
39 1	4935	12 Lumbar	41 5	5588	10 Lumbar	42 8	6925	2 Lumbar
39 8	5735	8 Lumbar	41 5	13600	9 Lumbar	42 10	4133	11 Lumbar
39 10	10850	5 Lumbar	41 7	5590	12 Lumbar	42 10	6510	11 Lumbar
39 11	4975	10 Lumbar	41 7	6430	12 Lumbar	42 10	7780	9 Lumbar
40 2	7352	9 Lumbar	41 8	5825	9 Lumbar	42 10	11442	10 Lumbar
40 3	3285	10 Lumbar	41 8	6180	10 Lumbar	43 2	7660	9 Thoracic
40 3	6940	12 Lumbar	41 8	6235	12 Lumbar	43 3	5798	5 Lumbar
40 3	6990	11 Lumbar	41 9	4420	12 Lumbar	43 4	3180	10 Lumbar
40 3	7115	6 Lumbar	41 9	7370	12 Lumbar	43 5	5110	1 Caudal
40 4	5960	8 Lumbar	41 10	6115	11 Lumbar	43 6	4960	5 Lumbar
40 4	10293	11 Lumbar	41 11	6620	11 Lumbar	43 6	7850	5 Lumbar
40 5	6020	7 Lumbar	41 11	8775	12 Lumbar	43 7	6750	11 Lumbar
40 5	10712	11 Lumbar	42 0	6700	8 Lumbar	43 8	4710	1 Caudal
40 6	8955	1 Caudal	42 2	3662	12 Lumbar	43 8	7580	4 Lumbar
40 6	9770	11 Lumbar	42 2	12200	9 Lumbar	44 1	7545	10 Lumbar
40 7	4028	11 Lumbar	42 3	5895	11 Lumbar	44 3	5810	6 Lumbar
40 7	5015	11 Lumbar	42 3	9060	12 Lumbar	44 3	7660	8 Lumbar
40 7	5965	11 Lumbar	42 4	5210	11 Lumbar	44 3	11968	9 Lumbar
40 9	5058	7 Lumbar	42 4	6100	7 Lumbar	44 6	7210	10 Lumbar
40 11	6120	1 Caudal	42 4	6305	9 Lumbar	44 9	4020	10 Lumbar
41 0	4918	11 Lumbar	42 4	8490	10 Lumbar	44 9	10200	11 Lumbar
41 0	6428	11 Lumbar	42 5	5760	12 Lumbar	44 11	6490	1 Lumbar
41 1	4355	12 Lumbar	42 5	7870	9 Lumbar	45 10	8155	3 Caudal
41 2	7660	7 Lumbar	42 6	4065	9 Lumbar			

(*b*) Full Epiphysial Fusion

Body Length	Mean Testis Weight (g)	Body Length	Mean Testis Weight (g)
ft in.		ft in.	
39 10	5175	43 8	6482
41 3	7450	44 6	11230
42 2	3660	44 6	10800
42 4	5570	45 6	5095

REPRODUCTION IN MALE HUMPBACK WHALE



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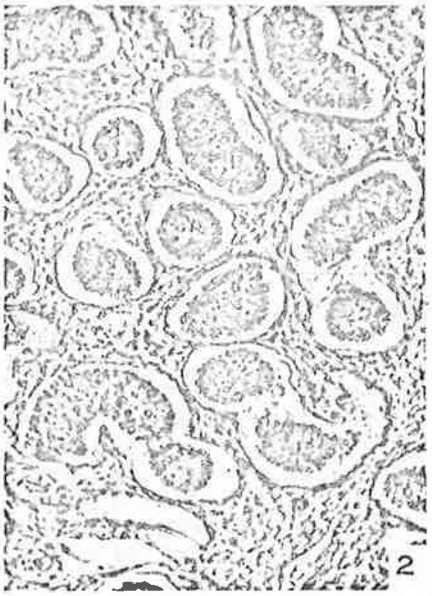

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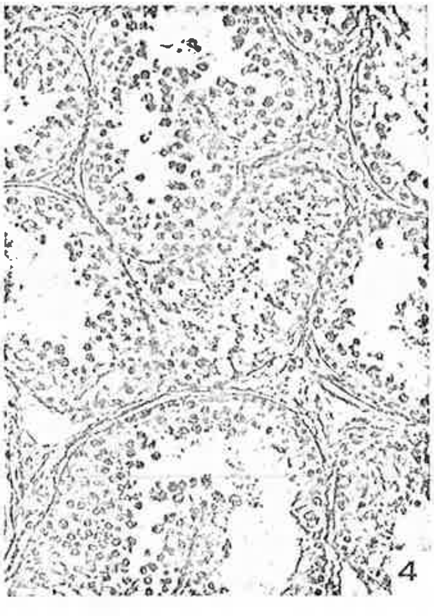

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Paper 2

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STUDIES ON THE OVARIES OF THE HUMPBACK WHALE *MEGAPTERA NODOSA* (BONNATERRE), ON THE WESTERN AUSTRALIAN COAST

By R. G. Chittleborough

Reprinted for the
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Australia

STUDIES ON THE OVARIES OF THE HUMPBACK WHALE, *MEGAPTERA NODOSA* (BONNATERRE), ON THE WESTERN AUSTRALIAN COAST

By R. G. CHITTLEBOROUGH*

(*Manuscript received October 19, 1953*)

Summary

Observations on the increase of ovarian weight in the female humpback whale cover stages from late foetal life until after the attainment of sexual maturity. Variations in ovary weight during different phases of the reproductive cycle are recorded.

Graafian follicles up to 0.13 mm in diameter have been found in the foetal ovary just prior to birth. These initially develop until from 11 to 29 mm (median value 20 mm) in diameter when the female reaches the maturing length range. At sexual maturity one of these follicles enlarges, exceeding 30 mm in diameter before rupture. After ovulation a corpus luteum is rapidly formed and if conception has taken place, this gland enlarges and remains active until parturition. After parturition there is rapid resorption of the corpus luteum to form a corpus albicans. Variations in the sizes and weights of functional corpora lutea are discussed.

There is considerable reduction in the diameters of Graafian follicles in late pregnancy to a median value of 6 mm. After parturition follicles enlarge so that in the ovaries of females in late lactation the largest follicles once more range from 11 to 29 mm in diameter with a median value of 20 mm.

In an ovulatory period of from June to November the maximum frequency of ovulations is in late July, though considerable numbers occur in August and September. On the available evidence most female humpback whales ovulate only once in their ovulatory period, a few ovulate twice, and extremely few three times.

I. INTRODUCTION

Observations upon the ovaries and a consideration of the reproductive cycle of the female humpback whale (*Megaptera nodosa* (Bonnaterre)) are recorded by Matthews (1937) in his general report upon humpback whales from the South Atlantic Ocean. Ovary weights were then available from very few females and, as Matthews indicated, these records were insufficient for detailed analysis. He pointed out that ovary weight increased at sexual maturity and assumed that this increase continued thereafter with some decrease in old age. With many more records of ovary weight, a more detailed analysis of such variations can be made.

Matthews referred to the enlarging of Graafian follicles at the approach of ovulation, saying that such follicles project further from the surface of the ovary, but gave no actual measurements.

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The size and weight of some functional corpora lutea were given in that report (Matthews 1937, p. 60) and the general statement was made that corpora lutea of pregnancy shrink rapidly after parturition, but the data were insufficient to analyse the variation in corpus luteum size at the different stages and the rate of resorption after parturition. Matthews distinguished the corpus luteum *"a"* (active) from the corpus luteum *"b"* (really a corpus albicans), stating that the transition was gradual. The present paper does not follow this designation but shows that after parturition the transition from an active corpus luteum (corpus graviditatum) to a corpus albicans is a rapid process.

From an analysis of foetal length Matthews concluded that the frequency of pairing was greatest between August and November with highest intensity in September. Using 11 months as the gestation period, he then indicated that the maximum frequency of births occurred in August. He stated that at birth calves were 4.5-5 m in length.

From the evidence available to him, Matthews concluded that the species bred once every 2 yr but that two pregnancies might sometimes occur in 3 yr; the much greater evidence now adduced supports this view. This evidence is based upon data gathered by the author at shore stations on the Western Australian coast in 1951 and 1952, supplemented by material collected by Whaling Inspectors of the State Fisheries Department from 1949 to 1952. The material from the three Western Australian whaling stations (at Point Cloates, Carnarvon, and Albany) for different years has been considered together.

This paper is mainly concerned with the macroscopic features of the ovaries and of the changes taking place in development from the late foetal stage until maturity, together with changes during the reproductive cycle. Considerable information concerning the time and frequency of ovulation has been acquired from the examination of over 300 pairs of ovaries from sexually mature females.

II. METHODS

Ovaries were examined as follows: after a superficial examination the whole ovary was sectioned transversely, using a meat slicer set to give sections of approximately 5 mm in thickness. It is considered that in this way no corpus albicans, however slight its remains may be, can be missed. Slices so taken are illustrated in Plates 2-6.

In these instances, as a result of prolonged immersion in formaldehyde solution, the follicular fluid had gelatinized and the tissues hardened, greatly assisting in the preparation of suitable slices for photography. Samples of foetal ovaries required for histological examination were fixed in Heidenhain's Susa fixative.

The results from the analysis of further ovarian material fixed for histological examination will be presented in a separate paper.

III. OVARY WEIGHT

(a) *Foetal Ovaries*

In general appearance the ovaries of humpback whales in the late foetal stage were similar to those of blue and fin whales described by Mackintosh and Wheeler (1929, p. 383), having a deep red colour and a much wrinkled surface. Table 1 shows the weights of the ovaries and the body lengths of late foetal humpback whales. Three of these foetuses are within or above the length range at birth as found by Matthews (see above), and their respective total ovary weights were 56.5, 107, and 173 g. Thus the present range of total ovary weight just prior to birth is 56.5-173 g.

TABLE 1

OVARY WEIGHTS FROM LATE FOETUSES

Length of Foetus (m)	Weights of Ovaries (g)		Total Weight of Ovaries (g)
2.82	26	26	52
3.78	50	55	105
4.34	48	55	103
4.54	28	28.5	56.5
4.91	85	88	173
5.03	49	58	107

(b) *Immature Ovaries*

As shown in Figure 1, ovary weight increases very little until a body length of about 34 ft is attained (with the exception of one immature female 29 ft 3 in. long which had a total ovary weight of 580 g). As sexual maturity approaches, ovary weight increases, but at the same time there is a greater individual variation. The maximum recorded total ovarian weight in an immature female was 3425 g. This is exceptionally high, but these ovaries appeared to be otherwise normal.

Owing to the wide range of values (Fig. 1) just prior to and after sexual maturation, it is not possible to distinguish mature and immature females on a basis of ovary weight as done by Jonsgard (1951) for the minke whale. Matthews (1937) noted that immature humpback ovaries seldom exceed 1½ lb (682 g), but Figure 1 of this paper shows that in immature females close to maturity the total weight of the ovaries not infrequently exceeds this value.

(c) *Mature Ovaries*

Figure 1 suggests that the increase in ovary weight with body length begun shortly before sexual maturity continues to some extent after the attainment of sexual maturity, but here the range of values is very wide.

When ovary weight is plotted against the number of corpora lutea (as an index of relative age) as shown in Figure 2, there is little evidence of increased ovary weight with relative age in sexually mature females. Mackintosh and Wheeler (1929) suggested that in fin and blue whales there is a decrease in ovary weight in older females (having 13 and 20 corpora lutea), but Figure 2 does not indicate any marked decrease in

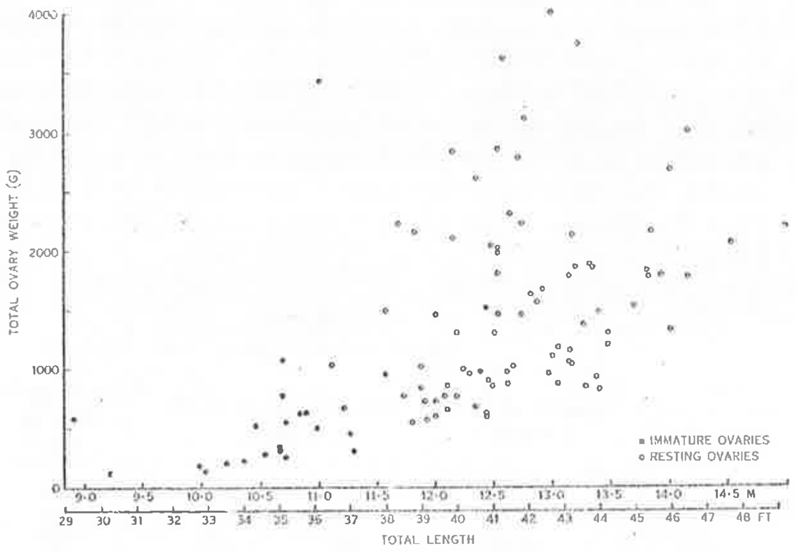

Fig. 1.—Total ovary weight and total length of females with immature and resting ovaries.

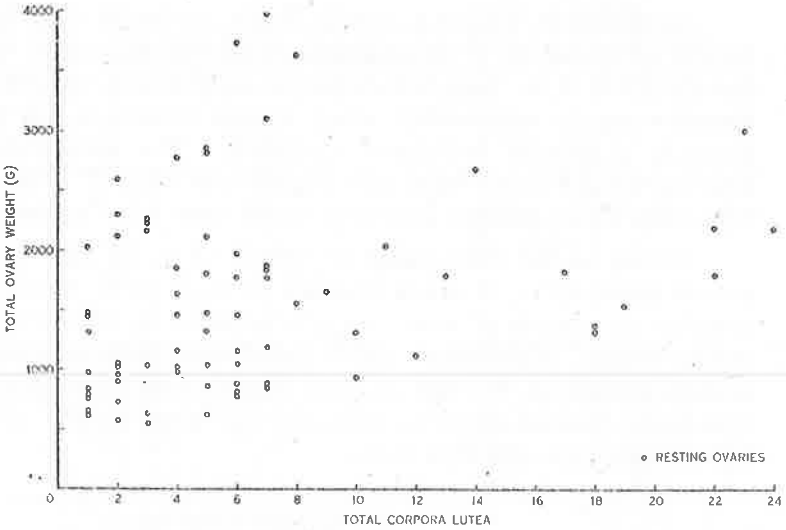

Fig. 2.—Total ovary weight and total corpora lutea of mature females with resting ovaries.

ovary weight of older female humpback whales having up to 24 corpora lutea in the ovaries.

The ovarian weights of mature females shown in Figures 1 and 2 are from ovaries in the resting phase, i.e. from females which were not pregnant, in the earlier stages of lactation, recently ovulated, or about to ovulate, so that possible variations in ovary weight within the reproductive cycle could be avoided in these figures. Ovaries of females in late stages of lactation are included in Figures 1 and 2 as these had all the features of resting ovaries; they possessed no corpus luteum showing signs of activity, and the Graafian follicles were of similar size to those in the ovaries of resting females (see Section IV (*e*) (iii)). The body length and total ovarian weight of each female shown in Figures 1 and 2 are listed in Appendix I.

TABLE 2

OVARY WEIGHTS AT VARIOUS STAGES OF THE REPRODUCTIVE CYCLE

Stage	Number of Females	Total Weight of Ovaries (g)				Weight of Single Ovaries (g)	
		Geom. Mean	Arith. Mean	Min.	Max.	Min.	Max.
Resting	20	1428	1547	625	2845	260	1525
Approaching ovulation	19	1322	1449	514	2400	184	1255
At ovulation	16	1033	1196	355	2795	160	1600
Early corpus luteum*	26	1378	1661	545	5505	172	2685
Late pregnancy	7	1992	2161	1120	3836	345	3204
Early lactation	5	1455	1624	845	3000	325	1845
Late lactation	56	1395	1590	550	3980	200	2095

* No embryo found but possibly some of these females may have just begun a pregnancy.

Table 2 shows the ranges of ovary weights of females in various stages of the reproductive cycle, together with the geometric and arithmetic means of paired ovary weights in the various stages. The distribution of ovary weights within each stage was unimodal and positively skewed so that for purposes of statistical analysis a logarithmic transformation was used to normalize the variation. The best estimate of the mean for each class is then found by working with transformed values, and this, in terms of the original data, corresponds to the geometric mean, which is used for the comparison of ovary weights in the stages shown in Table 2.

The above geometric means show little variation at the different stages, except that females which have just ovulated tend to have slightly lower total ovary weight, and females in late pregnancy a higher ovary weight than at other stages. But the range of values within all stages is so great that the differences in these geometric means are mostly not significant on the numbers of ovaries weighed. In the comparison of the geometric means of paired ovary weights in resting females and those at ovulation, by means of the *t* test, $t = 1.946$ on 34 degrees of freedom, which is not significant. Also in the comparison of the geometric means of paired ovary weights in resting females and those of late pregnant females, $t = 1.785$ on 25 degrees of freedom, which is not significant. However, in the comparison of the geometric means of paired ovary weights in females at ovulation and those in late pregnancy, $t = 2.677$ on 21 degrees of freedom, which is significant at the 2 per cent. level. The presence of a large functional corpus luteum in one ovary of each female in late pregnancy (weights of functional corpora lutea discussed under Section V (*b*)) tends to increase the total weight of the ovaries, although in late pregnant females the Graafian follicles are much reduced in size, as shown in Section IV (*d*).

IV. GRAAFIAN FOLLICLES

(*a*) *Follicles in Late Foetal Calves*

Sections of ovaries from late foetal female humpback whales show oogonia gathered in cavities (Pflüger's tubes) immediately below the ovarian surface. Slightly deeper in the ovarian tissue primary oocytes are abundant, each ovum being surrounded by a single layer of epithelial cells (Plate 1, Figs. 1, 2). In one primary oocyte the single layer of epithelial cells enclosed three ova (Plate 1, Fig. 3).

The largest early Graafian follicles in late foetuses are deepest in the ovaries, up to 2.5 mm from the surface. Some of these (Plate 1, Fig. 4) reach 0.13 mm in diameter, having an epithelial layer up to three cells thick and traces of a zona pellucida visible.

(*b*) *Immature, Resting, and Maturing Follicles*

In the examination of over 400 sets of humpback whale ovaries it has usually been found possible to distinguish maturing or mature Graafian follicles from well-developed but resting follicles. In larger immature females, and also in mature females not in late pregnancy or early lactation and not about to ovulate, the largest follicles are well developed but resting. Though these follicles do not project to any great extent from the general ovarian surface, they are sufficiently close to the surface to be seen in whole ovaries as purplish areas.

As a Graafian follicle approaches maturity it enlarges, projecting further from the surface of the ovary than the resting follicles (see Plates 2 and 3). The follicle wall becomes thinner on the projecting surface and fine blood vessels become visible in the wall. Except in a few older females where some follicles have degenerated into cysts, Graafian follicles at or over 30 mm in diameter are maturing and females with such follicles are approaching ovulation.

Figure 3 shows the diameter of the largest follicle in the ovaries plotted against the length of the female, using only immature females and mature females which were not pregnant, lactating, or recently ovulated. Upon a superficial examination, Figure 3 would appear to verify the findings of Nishiwaki and Oye (1948, p. 119), and Nishiwaki and Hayashi (1950, p. 156), who claimed that in mature blue and fin whales the size of the largest Graafian follicle is in proportion to the body length. However, in the humpback whales shown in Figure 3, those whose largest follicle was less than 30 mm in diameter must be considered apart from those whose largest follicle exceeded 30 mm in diameter as these two groups represent separate physiological conditions, the first being in the resting (anoestrus) condition, and the second approaching ovulation (prooestrus).

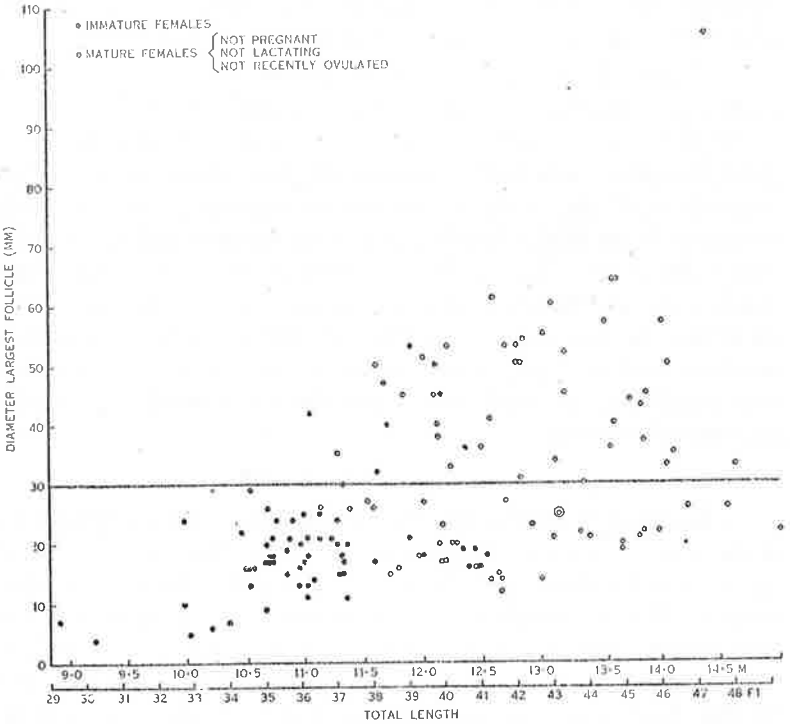

Fig. 3.—Diameter of largest Graafian follicle; immature and specified mature females.

Considering the immature females shown in Figure 3, those having a Graafian follicle at or over 30 mm in diameter are approaching their first ovulation. The shortest sexually mature female humpback whale found amongst Western Australian coast females was 35.5 ft long, while immature females up to 41.17 ft have been recorded. The immature females approaching their first ovulation (one Graafian follicle 30 mm or more in diameter) shown in Figure 3 are within this length range of 35.5-41.17 ft.

In the ovaries of immature females which are within this length range and have no maturing follicles, the largest Graafian follicle measured from 11 to 29 mm in diameter, with a median value of 20 mm. The upper sections in Plate 2 show the typical appearance across the ovaries of such an immature female.

Of the sexually mature females shown in Figure 3, the largest Graafian follicle in the ovaries of those which were not approaching ovulation measured from 12 to 28 mm in diameter, with a median value of 20 mm. Such females are classed in this report as resting or anoestrus females; they were not pregnant or lactating, had not recently ovulated, and were not approaching ovulation.

Figure 3 shows that some female humpback whales reach sexual maturity when between 36 and 39 ft long, while a number do not mature until from 40 to just over 41 ft. This may be due to different individual growth rates amongst females of the same age. Alternatively it is possible that this wide difference in lengths at sexual maturity may have resulted from some females reaching sexual maturity at 2 yr of age and others at 3 yr. The available records are only sufficient to suggest the possibility that some female humpback whales mature at 2 yr and others at 3 yr. In this regard Matthews (1937) suggested that sexual maturity was reached at 2 yr in humpback whales, but Mackintosh (1942) allowed the possibility of maturity being deferred until the third year in female humpback whales.

(c) *Ovulation*

Thirty-five of the female humpback whales examined on the flensing deck were found to have just ovulated, the blood-stained hole (from 4 to 13 mm in diameter) being immediately obvious on the surface of the ovary. When ovulation had occurred immediately prior to the death of the female and the ovary was then cut across the collapsed follicle the latter was found to contain no liquid, but the lining showed wrinkling at the first stages of the folding which would have led to the formation of a corpus luteum. At a slightly later stage as the folding of the follicular wall becomes more obvious the centre of the ruptured follicle is often filled with a translucent gel, presumably the tertiary liquor folliculi of Brambell (1930, p. 121). Such a stage is shown in Plate 4.

There is a very wide range of follicle diameter immediately after rupture, from 22 to 60 mm (median 37 mm) but it is doubtful whether these diameters can be compared directly with those of turgid follicles just prior to rupture. The smallest burst follicle, 22 mm in diameter, was possibly not normal as here two follicles (22 and 23 mm) had burst simultaneously. This was one of two cases of double ovulations recorded in the present study. Omitting this double ovulation, only four of the 35 females taken immediately after ovulation had burst follicles below 30 mm in diameter (26, 27, and 28 mm) and these when turgid prior to rupture would very probably have exceeded 30 mm in diameter, in agreement with the observation in part (*b*) above that maturing Graafian follicles were from 30 mm in diameter. Figure 3 shows that the upper limit of follicle diameter at ovulation is over the 60 mm maximum recorded for a burst follicle as one apparently normal mature follicle reached 105 mm in diameter. This follicle had a very thin, almost transparent area on the surface, indicating it was close to the point of rupture.

(*d*) *Graafian Follicle During Pregnancy*

Although several very small embryos have been found in east Australian coast female humpbacks, no records of early pregnancy are available as yet from females taken off the western coast, despite careful searching of the uteri of females whose ovaries contained a developing corpus luteum. Females in late pregnancy were not of infrequent occurrence. The diameters of the largest Graafian follicle in each set of ovaries from 45 of these are shown in Table 3.

TABLE 3

DIAMETER OF LARGEST GRAAFIAN FOLLICLE IN LATE PREGNANT FEMALES

Diameter Largest Follicle (mm)	No. of Late Pregnant Females	Diameter Largest Follicle (mm)	No. of Late Pregnant Females
2	2	10	2
3	5	11	2
4	3	12	—
5	9	13	—
6	10	14	—
7	4	15	1
8	4	16	—
9	2	17	—
		18	1

Table 3 shows that female humpback whales in late pregnancy have much reduced Graafian follicles (median value 6 mm), well below the range in resting mature females (median value 20 mm). In only two cases of late pregnancy were follicles approaching the size in resting females (diameters 15 and 18 mm respectively) and these, like all follicles in the ovaries of late pregnant females, appeared to have undergone a good deal of resorption. Generally follicles are so reduced that there is little more than a thickened wall with very little space for the liquor folliculi. These reduced follicles do not project from the wall of the ovary and are not at all obvious, as can be seen from Plate 6.

This marked reduction in follicle size at late pregnancy in the humpback whale is not in agreement with the results in blue and fin whales recorded by Mackintosh and Wheeler (1929) who stated that in those whales "There are invariably many enlarged follicles in the ovaries of pregnant whales and these range from 40 mm. to 50 mm. in diameter to 10 mm. and less". Also Nishiwaki and Oye (1948) recorded large follicles in pregnant blue and fin whales, and indicated that the largest Graafian follicles exceeded those of resting females. But both British and Japanese workers obtained their records from Antarctic waters, where most of the pregnant females would have been in earlier stages of pregnancy. It is possible that resorption of follicles would not have been evident until later stages. The large follicles in early pregnancy reported by both sets of workers had apparently matured just before the females' present pregnancies and had not yet atrophied. Indirect evidence of reduction in follicle size in late pregnancy in blue and fin whales is afforded by Mackintosh and Wheeler's observation that follicles were reduced during lactation.

(e) *Graafian Follicles During Lactation*

(i) *Early Lactation.*—Diameters of the follicles in the early stages of lactation are available from three females, the largest follicles being 6, 8, and 26 mm respectively. The first two are within the range of follicle size found in late pregnancy (see above) and are to be expected soon after parturition, while in the third this larger follicle was presumably an example of one follicle maturing just before the onset of a pregnancy resulting from a previous ovulation and while a good deal of resorption may have taken place, this follicle remained above normal size during pregnancy and in lactation up to the time the female was killed. Mackintosh and Wheeler (1929, p. 388) recorded that in blue and fin whales, "during lactation one or two large follicles are found but the smaller ones are no longer visible" (on the surface of the ovary).

(ii) *Mid Lactation.*—At this stage follicles have begun to increase in size, but the largest are still in the lower part of the range found in the ovaries of resting females, the largest follicles from three females in mid lactation being 11, 15, and 18 mm respectively.

(iii) *Late Lactation.*—Maximum follicular diameters are available from 60 normal cases of this stage, with a range of 10-50 mm, and in a few cases ovulation had very recently taken place, so that in some female humpback whales maturation of follicles or even ovulation takes place without a resting (anoestrus) phase following lactation.

These females in late lactation could be divided into two groups, those with no maturing follicles, and those with follicles maturing or recently burst; 82 per cent. were in the former group, having a maximum follicular diameter ranging from 10 to 28 mm with a median value of 20 mm, the same as that found in the ovaries of resting females, while 18 per cent. had maturing follicles (diameters 35-50 mm) or had recently ovulated.

One anomalous case of late lactation was recorded in which the female was pregnant. Here the largest follicle was reduced to 11 mm in diameter. This female (No. 54 of the Carnarvon station's 1952 catch) was carrying a 9 ft 3 in. foetus when killed in mid June. This was a rather small size for that month, but this might be expected in an unusual case of a further pregnancy beginning shortly after the previous parturition (see Section VI(*c*)).

(*f*) *Ovarian Cysts in Older Females*

Four Western Australian coast females were found to have large cysts attached to the ovaries. These females were relatively old, there being from 27 to 34 'corpora lutea' in the ovaries and full physical maturity had been reached in the three whose vertebral epiphyses were examined. It is thought that these cysts were degenerate Graafian follicles. Only one of four physically mature females examined had normal ovaries with no cysts attached and these showed a total of 38 'corpora lutea'.

Data concerning the four cases where ovarian cysts were present are summarized as follows:

No. 163 from Carnarvon, 1951:

Total length 45.5 ft; 34 'corpora lutea', one recently developed. Several thin-walled liquid-filled cysts hanging away from both ovaries. Largest cyst on one ovary 72 mm in diameter while largest on the second ovary was 100 mm. The liquid from the larger cysts on the second ovary weighed 1140 g. It was difficult to decide which were smaller cysts and which were normal Graafian follicles. A fully physically mature female.

No. 599 from Carnarvon, 1951:

Total length 43.0 ft; 29 'corpora lutea', one very recently developed. Several thin-walled cysts (filled with clear liquid) to 65 mm in diameter hanging from the ovaries. Fully physically mature.

No. 313 from Point Cloates, 1952:

Total length 45.2 ft; 27 'corpora lutea'; none recent. Large thin-walled cysts to 150 mm in diameter containing clear liquid. Graafian follicles 15-20 mm in diameter were thick-walled and possibly non-functional. A fully physically mature female.

No. 363 from Point Cloates, 1952:

Total length 43.5 ft; 29 'corpora lutea'; none recent. This female had just ovulated. Several thin-walled cysts 36-71 mm in diameter. Vertebral epiphyses not examined.

V. CORPORA LUTEA

(*a*) *Early Development After Ovulation*

Growth and folding of the follicular epithelium with the formation of luteal tissue begins very soon after ovulation so that the vesicle remaining after rupture of the Graafian follicle is soon filled with luteal tissue, although some translucent gel sometimes occupies the centre of the newly formed corpus luteum. Plate 4 shows an early stage in this process. A recently developed corpus luteum can readily be distinguished from later stages, the outer membrane being very thin with numerous blood vessels visible immediately beneath it. The luteal tissue is soft, pale, and expanded in contrast to the firmer yellow tissue in late pregnancy and early lactation. Plate 5 shows a section through a recently developed corpus luteum.

The initial size of a corpus luteum after formation is dependent upon the size of the follicle at ovulation. It was shown above that maturing follicles reach 30 mm in diameter before rupture. This is in agreement with measurements of early corpora lutea, the smallest having a diameter of 32 mm. But once formed, the corpus luteum continues to develop, increasing in size. Figure 4 shows the maximum diameter of the recently formed corpora lutea from Western Australian coast female humpbacks and the date upon which these females were killed. It is seen that larger glands are found later in the season. The broken line in Figure 4 linking the largest corpora lutea found in each month indicates a probable growth curve of those corpora lutea developed from ovulations earlier in the season. During the first 2 months of development the corpus luteum steadily increases in size, the growth then slowing down as the maximum diameter approaches the range found in corpora lutea of late pregnancy.

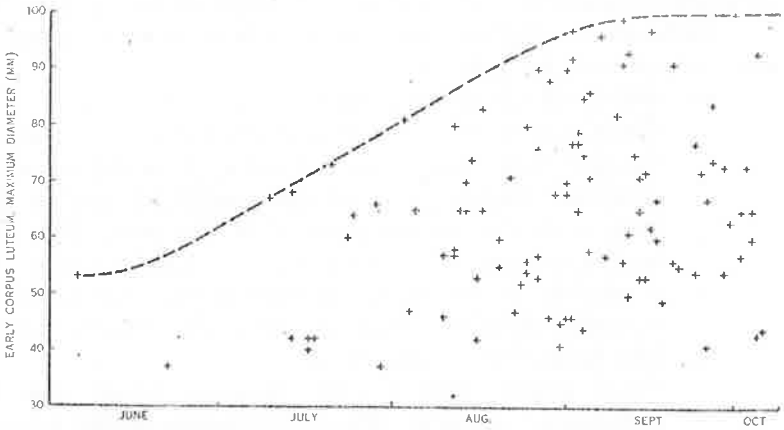

Fig. 4.—Maximum diameter of early corpora lutea.

The small recently formed corpora lutea found late in the catching season (late September and early October, see Fig. 4) indicate that ovulation continues throughout the winter and early spring.

In each case of an early corpus luteum shown in Figure 4 the uterus of the female was carefully searched for an early embryo but none was found. However, if pregnancy had begun the embryo would have been very small, and in the short time available for examination of the uterus it could easily have been missed. Because of this failure to establish whether or not pregnancy had begun in the individuals represented in

Figure 4, it is not known how far development of a corpus luteum proceeds if ovulation is not followed by pregnancy.

(*b*) *Corpora Lutea of Pregnancy* (*Corpora Graviditata*)

All pregnant females from the Western Australian coast so far examined were in late pregnancy (foetuses from 9 ft 3 in. to 17 ft 6 in.).

TABLE 4

FEMALES IN LATE PREGNANCY: OVARY AND FOETUS RECORDS

Functional Corpus Luteum			Ovary Weights (g)		Total Corpora Lutea	Foetus	
Weight (g)	Dimensions (mm)	Mean Dia. (mm)				Sex	Length
305	106 × 79 × 74	86	—	—	2	♀	3.31
327	96 × 93 × 74	88	—	—	4	♂	3.93
422	102 × 97 × 78	92	—	—	38	♂	4.30
450	107 × 86 × 85	93	940	343	7	♂	3.90
633	121 × 113 × 81	105	—	—	2	♂	4.36
643	144 × 120 × 67	110	—	—	30	♂	4.27
657	116 × 100 × 95	104	—	—	6	♂	3.60
770	132 × 117 × 100	116	—	—	10	♂	4.54
822	136 × 134 × 87	119	—	—	16	♀	5.06
860	130 × 110 × 92	111	1765	530	10	♀	4.30
860	137 × 123 × 95	118	—	—	3	♀	3.78
867	147 × 121 × 97	122	—	—	9	♂	4.02
873	150 × 103 × 96	119	—	—	7	♂	5.27
876	124 × 111 × 110	115	—	—	5	♀	4.91
970	145 × 125 × 91	120	1890	640	17	♀	4.15
1005	145 × 117 × 107	123	1755	760	14	♀	2.83
1082	135 × 130 × 105	123	—	—	22	♀	5.03
1194	162 × 152 × 88	134	—	—	15	♀	4.54
1215	140 × 138 × 106	128	—	—	8	♂	4.63
1231	140 × 127 × 100	122	—	—	8	♀	5.24
1395	170 × 136 × 118	141	—	—	24	♀	3.60
1412	173 × 157 × 95	142	—	—	14	♂	4.33
1449	163 × 126 × 123	137	—	—	18	♂	5.33
1475	160 × 135 × 130	142	—	—	11	♀	4.48
1597	185 × 165 × 85	145	—	—	25	♀	4.36
1695	165 × 158 × 117	147	—	—	7	♂	4.54
1711	155 × 145 × 130	143	—	—	21	♂	3.90
1945	196 × 162 × 125	164	—	—	7	♀	4.66
2185	205 × 160 × 100	155	3204	632	7	♂	4.27
Median of mean dimensions of corpora lutea		122					
Mean of mean dimensions of corpora lutea		123					

The functional corpora lutea of these females showed great variability in weight and size, ranging from 305 g (106 by 79 by 74 mm) to 2185 g (205 by 160 by 100 mm). Details of the cases of late pregnancy where the functional corpus luteum was weighed are shown in Table 4. The three measurements of a corpus luteum were obtained by first taking the greatest diameter and then the lengths of the two axes at right angles to this.

The weight of the corpus luteum in late pregnancy is not a function of total ovary weight. Functional corpora lutea weights were from 35 to 57 per cent. of the total ovary weight.

The sex of the near-term foetus was found to have no bearing on this wide variation in functional corpora lutea weight. In 15 cases of late pregnancy where the foetus was a male the functional corpus luteum ranged from 327 to 2185 g, with a mean weight of 1021 g, while in 14 cases with a female foetus the corresponding range was 305-1945 g, mean 1116 g.

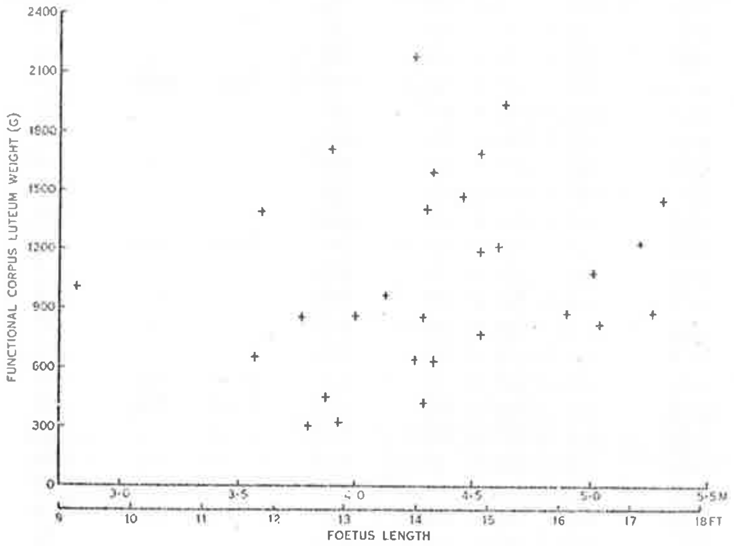

Fig. 5.—Weight of functional corpus luteum and foetal length.

Mackintosh and Wheeler (1929, p. 388) stated that there was some indication in fin and blue whales that the corpus luteum of pregnancy increased in size up to the stage when the foetus measured 1 m, and thereafter decreased, probably up to the end of gestation. In Section V (*a*) an early increase in corpus luteum size was shown (Fig. 4) but the state of pregnancy was not established. In Figure 5 the weight of the functional corpus luteum is shown against length of foetus, using the records from Table 4. This scatter diagram does not indicate any relationship between functional corpus luteum weight and the stage of gestation (the latter based on foetal length).

Table 5 shows data from female humpbacks in early pregnancy extracted from Matthews's (1937) report. The range of the functional corpora lutea weights in early pregnancy from these South Georgian specimens was only slightly below that shown in Table 4 for Western Australian coast females in late pregnancy.

In Figure 6 the mean diameters of the functional corpora lutea have been plotted against foetal length, including the data from Tables 4 and 5. This figure shows little variation of size of functional corpora lutea with the stage of gestation, unless perhaps a slight increase in functional corpus luteum size in advanced pregnancy. Thus the evidence from corpora lutea weights and measurements does not agree with the decrease in size of the functional corpus luteum as pregnancy advances suggested by Mackintosh and Wheeler for blue and fin whales

TABLE 5

FEMALES IN EARLY PREGNANCY; SOUTH GEORGIA (FROM MATTHEWS 1937)

	Functional Corpus Luteum		Ovary Weights (g)		
	Mean Diameter (mm)	Weight (g)	Ovary Carrying Corpus Luteum	Inactive Ovary	Foetus Length (cm)
	66	—	—	—	68
	78	270	790	—	28
	95	—	1814	—	38
	100	400	740	340	76
	110	—	—	—	75
	130	1050	1640	680	70
	140	—	—	—	51
	160	1810	2680	620	4
Mean	110				

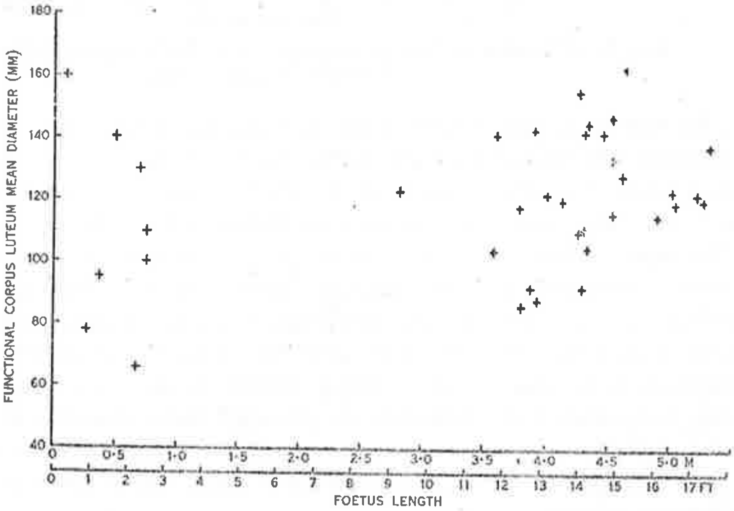

Fig. 6.—Mean diameter of functional corpus luteum and foetal length.

On the available evidence there would appear to be some relationship between the weight of the functional corpus luteum and the age of the late pregnant female, using the total number of corpora lutea as an index of relative age. In Figure 7 the weight of the functional corpus luteum is shown against the total corpora lutea in the ovaries of 29 females in late pregnancy. The weight of the functional corpus luteum in these tends to increase with increasing numbers of corpora lutea but is again low in relatively old females (having 30 and 38 'corpora lutea' in the ovaries).

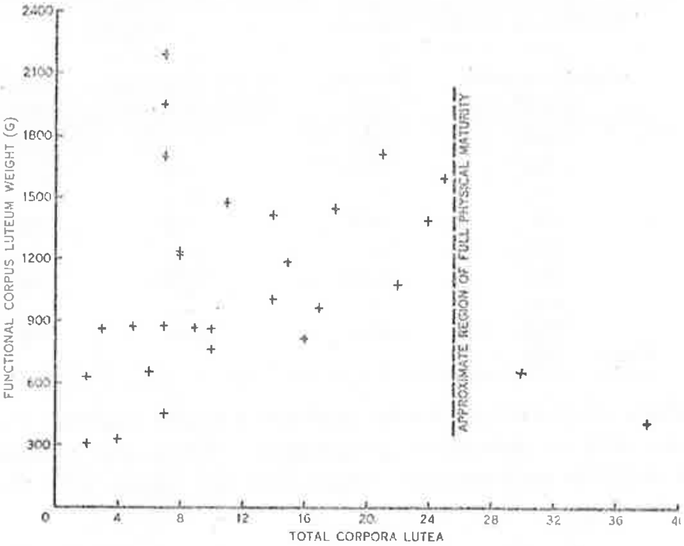

Fig. 7.—Females in late pregnancy: functional corpus luteum weight and total corpora lutea.

In one pregnant female two corpora lutea had all the characteristics of normal functional corpora lutea, though both were smaller than usual. This female was carrying a male foetus 3.96 m (13.0 ft) long. In one ovary the functional corpus luteum measured 98 by 94 by 54 mm, while in the other ovary the functional corpus luteum measured 76 by 75 by 57 mm. Respective ovary weights were 780 and 765 g, unusually close together for a case of late pregnancy as seen from ovary weights in Tables 4 and 5. In this case probably two Graafian follicles had burst simultaneously, one ovum having failed to be fertilized, or the zygote being lost, but both follicles developing into functional corpora lutea, neither of which reached the size range of single functional corpora lutea in late pregnancy. Such a condition must be regarded as rare in the humpback whale.

(c) *Resorption of the Corpus Luteum During Lactation*

After parturition the resorption of the functional corpus luteum (corpus graviditatum) is very rapid. Table 6 shows the range and mean size of the corpora lutea in stages from the active state (in late pregnancy) until late in lactation.

In early lactation the resorption of the corpus graviditatum has already begun, as indicated by a decrease in size. But the gland still hangs away from the main portion of the ovary and has a tight, relatively thin outer membrane with many blood vessels below this. The luteal tissue still has the wide expanded convolutions as seen during late pregnancy. By mid lactation the resorption of the corpus luteum is well advanced (Table 6). Blood vessels are still visible in the enclosing capsule which is now thickening with fibrous tissue. By the last few weeks of lactation the resorption of the corpus luteum has proceeded so far that it seldom shows any signs of its earlier activity and must now be classed as a corpus albicans. The resorbed luteal tissue is now enveloped in a thick fibrous capsule and does not usually project far from the ovarian surface. In fact it is often difficult in late lactation to determine which of the corpora albicantia had been most recently functional so that for the measurements used for late lactation in Table 6

TABLE 6
RESORPTION OF FUNCTIONAL CORPORAL LUTEA

	Average Diameter (mm)
(i) Corpora lutea in late pregnancy	
Largest 196 × 162 × 125 mm	164
Smallest 106 × 79 × 74 mm	86
Mean of average diameters from 29 corpora lutea of late pregnancy	123
(ii) Corpora lutea in early lactation	
Dimensions (mm) 140 × 110 × 90	113
111 × 97 × 75	94
95 × 70	83
Mean of average diameters of 3 corpora lutea of early lactation	97
(iii) Corpora lutea in mid lactation	
Dimensions (mm) 92 × 84 × 80	85
97 × 73 × 68	80
102 × 78 × 58	79
91 × 72 × 67	77
89 × 81 × 61	77
83 × 64	74
Mean of average diameters of 6 corpora lutea of mid lactation	79
(iv) Corpora lutea in late lactation (now corpora albicantia)	
Largest 86 × 76 × 63 mm	75
Smallest 40 × 27 mm	33
Mean of average diameter of 62 corpora lutea of late lactation	50

the largest corpus albicans has been taken as the remnant of the most recently functional corpus luteum.

From this stage, further resorption of the corpus albicans is very slow and although some may be reduced to a mean diameter of 6 mm there is little doubt, as shown by Mackintosh (1942, p. 220), that in whales the corpora albicantia persist, if not throughout life, then at least until long after physical maturity has been reached.

VI. Time and Frequency of Ovulation

(a) *Time of Ovulation*

Table 7 summarizes the variations in the condition of the ovaries as found in 290 mature Western Australian coast females, excluding females in late pregnancy and early lactation. Those in late lactation have been included in the respective column indicated by the state of the ovaries.

Table 7

STATE OF THE OVARIES OF MATURE FEMALES IN 10-DAY PERIODS, EXCLUDING FEMALES IN LATE PREGNANCY AND EARLY LACTATION

Ten-day period	Total No.	Resting Ovaries		Maturing Follicle		Burst Follicle		Early Corpus Luteum	
		No.	%	No.	%	No.	%	No.	%
June 1-10	22	20	90.0	1	4.5	0	—	1	4.5
June 11-20	25	25	94.0	2	8.0	0	—	0	—
June 21-30	24	15	62.5	8	33.3	0	—	1	4.2
July 1-10	18	6	33.3	9	50.0	2	11.1	1	5.6
July 11-20	35	4	11.4	22	62.9	6	17.1	6	17.1
July 21-30	17	2	11.8	6	35.3	8	47.1	4	23.5
July 31-Aug. 9	13	1	7.7	8	61.5	3	23.1	5	38.5
Aug. 10-19	24	3	12.5	7	29.2	4	16.7	14	58.3
Aug. 20-29	25	5	20.0	7	28.0	5	20.0	13	52.0
Aug. 30-Sept. 8	29	3	10.3	9	31.0	2	6.9	21	72.4
Sept. 9-18	25	0	—	6	24.0	4	16.0	19	76.0
Sept. 19-28	20	4	20.0	4	20.0	0	—	13	65.0
Sept. 29-Oct. 8	13	1	7.7	4	30.8	0	—	11	84.6

The above percentages are graphed in Figure 8 to indicate the sequence of events from June to early October in the ovaries of mature females which were not in advanced pregnancy nor had recently given birth to a calf. Figure 8 shows that, off the Western Australian coast for the greater part of June, almost all (over 90 per cent.) of the above described class of mature females have ovaries in the resting condition, though in a small percentage of cases a maturing follicle or an early corpus luteum is present. Over 70 per cent. of these mature females with ovaries in the resting state taken in early June were in late stages of lactation. At the end of June, as the proportion of females with resting ovaries began to decrease, so the numbers of females in late lactation began falling, while the proportion of females with a maturing Graafian follicle in the ovaries increased.

By mid July only a small part of this group of mature females had resting ovaries, and numbers in this group remained relatively low for the rest of the winter and spring. But in mid July the proportion of females having a mature follicle in the ovaries reached a maximum, followed by a drop in the latter part of July when the frequency of occurrence of ruptured follicles reached its maximum. A secondary increase of females with a mature follicle early in August was not followed by a rise in ovulation frequency. This may be due to a movement of part of the population at this time. It has been shown (Chittleborough 1953) that increasing numbers of humpbacks turn southwards during August, while many are still travelling up the coast. However, while females with a mature follicle were less frequent from mid August to October, Figure 8 indicates that maturation of follicles and ovulation continue on a lessened scale until at least early October.

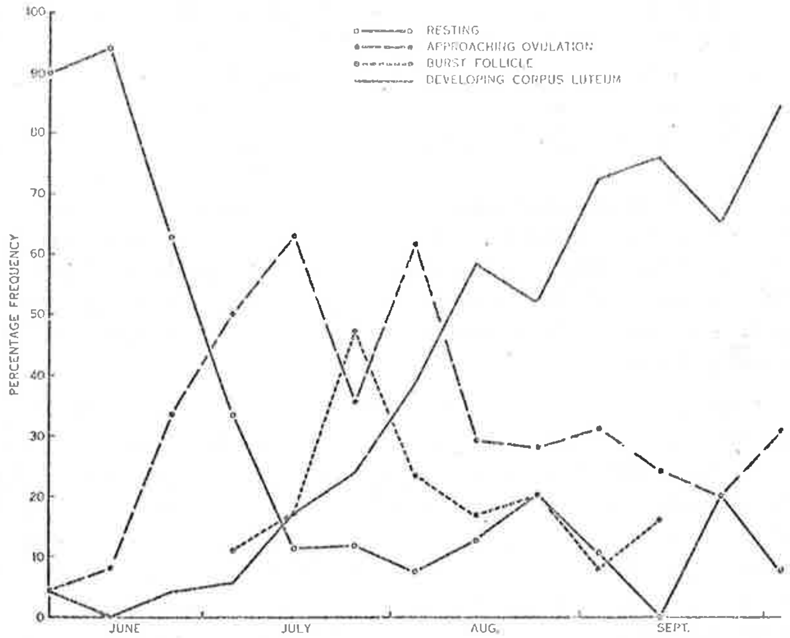

Fig. 8.—State of ovaries in mature females excluding late pregnant and early lactating females.

The maximum frequency of occurrence of ruptured follicles in the latter half of July was at a lower level than other stages (Fig. 8) owing to the fact that the transformation of a mature Graafian follicle to an early corpus luteum is a relatively fast process so that fewer females are killed in just this phase.

The proportion of females with a developing or recently developed corpus luteum, initially very low in June, increased in July and after the July maxima of maturing and burst follicles, became higher from August to October, by which time over 80 per cent. of the mature females not in late pregnancy or early lactation had at least one early corpus luteum in the ovaries.

From the above it would appear that off the Western Australian coast in June the mature female humpback whales (excluding those in late pregnancy and early lactation) are generally in late lactation, sometimes having ceased lactating, but with ovaries in the resting condition. In late June and early July, as lactation terminates (and sometimes before, as discussed below), maturation of at least one Graafian follicle usually begins. This is followed by ovulation generally in the latter half of July. But after this period of maximum frequency of ovulations, ovulation continues to occur with lesser frequency up to at least early October. The presence of an occasional female with an early corpus luteum in early June shows that ovulation does occur in a few females in late May or early June.

Since by the end of the catching season over 80 per cent. of the mature females which were not about to give birth, or had just given birth to a calf, had ovulated during the catching season (as judged by the presence of an early corpus luteum), a 2-yr breeding cycle can be inferred for the majority of female humpbacks, i.e. pregnancy occupying most of the first year (as given by Matthews), lactation extending over the greater part of the second year, with ovulation occurring at the end of the second year. On present evidence it appears that lactation occupies a greater period (a total of approx. 10 months) than that indicated by Matthews (1937) for female humpbacks in the South Atlantic Ocean.

(b) *Frequency of Ovulation During the Ovulatory Period*

As shown by Figure 8, ovulation first occurs early in June and continues throughout the Australian catching season, possibly into November, though no records are available for this month. June to November has been taken as the ovulatory period. Table 8 has been drawn up to indicate ovulation frequency in 10-day periods from June to October, using only mature females which were approaching ovulation or had ovulated once or more during the season in which they were killed. From this table the curves in Figure 9 have been drawn to show the trends in the ovaries of ovulating females as the catching season progressed. The frequency of occurrence of ovaries with one maturing follicle (curve *F*) decreased from June to July as the frequency of occurrence of ovaries bearing the first corpus luteum rose (curve *C*). These two curves cross in the latter half of July, in close agreement with the time of maximum ovulations shown in Figure 8.

For analysis of the frequency of ovulation during the catching season off the Western Australian coast, the positions of the curves of Figure 9 at the end of the season must be compared. By early October, Figure 9 shows that 62 per cent. of the ovulating females had ovulated once with no further follicles maturing (curve *C*). In a further 10 per cent. (curve *F*) the first maturing follicle of the season was present. It is possible that most of these females with a maturing follicle would have ovulated once before returning to the southern summer feeding grounds, so that a total of 72 per cent. of the ovulating females could have ovulated no more than once during the ovulatory period (June to November).

TABLE 8

WESTERN AUSTRALIAN COAST FEMALES OVULATING OR APPROACHING OVULATION: OVULATION FREQUENCY FROM JUNE TO OCTOBER

10-Day Period	Total Ovulating (or about to ovulate)	Approaching First Ovulation of Season		Ovulated Once: No Further Follicles Maturing		Ovulated Once: Second Follicle Maturing		Ovulated Twice: No Further Follicles Maturing		Ovulated Twice: Third Follicle Maturing	
		No.	%	No.	%	No.	%	No.	%	No.	%
June 1-10	2	1*	50	1*	50	—	—	—	—	—	—
June 11-20	2	2	100	—	—	—	—	—	—	—	—
June 21-30	9	8	89	1	11	—	—	—	—	—	—
July 1-10	12	9	75	3	25	—	—	—	—	—	—
July 11-20	31	19	61	9	29	3	10	—	—	—	—
July 21-30	15	4	27	8	53	2	13	1	7	—	—
July 31-Aug. 9	12	4	33	4	34	4	33	—	—	—	—
Aug. 10-19	21	2	10	14	66	5	24	—	—	—	—
Aug. 20-29	20	2	10	12	60	5	25	1	5	—	—
Aug. 30-Sept. 8	26	3	12	17	65	6	23	—	—	—	—
Sept. 9-18	25	2	8	16	64	4	16	3	12	—	—
Sept. 19-28	15	3	20	10	66	1	7	1	7	—	—
Sept. 29-Oct. 8	12	1	8	7	58	2	17	1	8	1	8

* Numbers within this period too small to be significant.

In early October 12 per cent. of the ovulating females had ovulated once and had a second follicle maturing. If these females had conceived at the first ovulation, this second maturing follicle would atrophy, but if conception had not taken place it would probably have burst before these females returned to the Antarctic feeding grounds. Only 8 per cent. of the ovulating females had ovulated twice during the season by early October, and showed no sign of further maturing follicles (curve *CC*).

A further 8 per cent. had ovulated twice by early October and had a third follicle maturing (curve *CCF*), so that three ovulations in one season could have occurred in this group if conception had not already taken place.

The situation amongst ovulating females by the beginning of October was that a minimum of 62 per cent. (from curve *C*) had ovulated once only, with a possible maximum of 84 per cent. (from curves *C* + *F* + *CF*) which may not have ovulated more than once during the season. A minimum of 16 per cent. (curves *CC* + *CCF*) had ovulated twice during the season with a possible maximum of 28 per cent. (curves *CC* + *CCF* + *CF*), while from 0 to 8 per cent. might have ovulated three times during the ovulatory period.

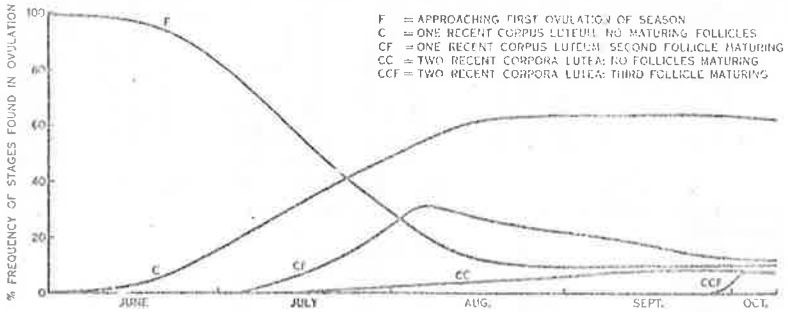

Fig. 9.—Ovulating females only: stages in ovulation.

Thus between June and October the proportions of ovulating females which ovulated once, twice, and three times respectively were variable, mainly because, of the cases where ovulation had already occurred, another follicle was maturing, but the fate of the previously discharged ovum was unknown. However, it can be said that the greatest proportion of the female humpbacks during their ovulatory period ovulated only once, few ovulating twice, and on present evidence, rarely three times.

From the present evidence it appears that the mean number of ovulations per female humpback during the ovulatory period was only slightly above 1, less than the 1.9 for blue, and 1.8 for fin whales as estimated by Dr. N. Peters (see Mackintosh 1942, p. 227). Matthews's estimate of five ovulations for each sexual cycle of 2 yr in female humpbacks appears to have been far too high.

The analyses above are based upon the assumption of a 2-yr breeding cycle in female humpbacks. As indicated earlier, most of those mature females not in late pregnancy or lactating do ovulate between June and November, but as shown in Figure 8, a small part (a little over 10 per cent.) of these females show no sign of ovulating during the general ovulatory period. In these one of two possibilities might apply. It may be that occasionally mature female humpback whales undergo a lengthened period of anoestrus so that instead of a normal 2-yr sexual cycle, the cycle extends over 3 yr. The second possibility is that these females with ovaries resting throughout the period when ovulation should normally have taken place might be out of phase and could ovulate during the summer while feeding in southern waters. This latter explanation is the most likely, as Matthews recorded one humpback foetus from South Georgia 0.31 m (12¼ in.) long in May when foetuses were generally about 2.7 m (8 ft 10 in.) long. Also at the Point Cloates (W.A.) station a foetus 1.45 m (4 ft 9 in.) long has been recorded in July, when foetuses were generally in the region of 4.2 m (13 ft 9 in.). In both of these cases, conception must have taken place in December or January. Mackintosh and Wheeler indicate that in blue and fin whales ovulation (and possibly conception) may occasionally take place during the southern summer.

(c) *Ovulation During Lactation*

As indicated in Section VI(*a*), over 70 per cent. of the mature females with ovaries in the resting state taken in early June were in late stages of lactation. Generally lactation terminated before Graafian follicles began maturing, but occasionally during the last stages of lactation (June or early July) a mature follicle was found in the ovaries, and sometimes, generally when lactation appeared to have been continued somewhat later than usual, ovulation had even taken place and an early corpus luteum was present in the ovaries.

Since present evidence strongly suggests that lactation in female humpbacks extends longer than the 5 months indicated by Matthews, generally continuing until the first part of the succeeding ovulatory period, it might be expected that occasionally a follicle matures or even ovulation takes place, shortly before the termination of lactation.

One case has been found amongst Western Australian coast females where ovulation had very recently occurred in a female in a fairly early stage of lactation. This was whale No. 196 of the Carnarvon station's 1951 catch, killed on August 2. A recently functional corpus luteum measuring 102 by 78 by 58 mm was found in one ovary, while one Graafian follicle 34 mm in diameter had recently burst and a second follicle 36 mm in diameter was maturing. As Matthews indicated, ovulation during early lactation could give rise to two pregnancies in 3 yr, but this must be regarded as abnormal in female humpback whales.

Further evidence for two pregnancies occasionally occurring in 3 yr was obtained from whale No. 54 of the Carnarvon station's 1952 catch. This female, killed on June 15, was carrying a foetus 9 ft 3 in. long, yet was lactating copiously. This case must have been similar to that of No. 196 discussed above: ovulation (followed by pregnancy in this instance) taking place shortly after parturition, so that by the following June this female was in relatively advanced pregnancy yet still lactating in association with the previous pregnancy.

(*d*) *Multiple Ovulations*

From over 330 mature female humpback whales examined in detail on the Western Australian coast, two examples of multiple ovulations have been found. One of these has already been described in Section V(*b*). In this, two follicles had apparently burst simultaneously, one from each ovary, only one ovum being successfully fertilized, so that when this female was killed in late pregnancy two functional corpora lutea were present but only one foetus. Similar occasional examples of females with more than one functional corpus luteum have been recorded by Wheeler (1930) in fin whales. The second has been mentioned in Section IV(*c*). This female (No. 448 of the Point Cloates station's 1952 catch), 38 ft 5 in. long, having one corpus albicans in the ovaries, had two very recently burst Graafian follicles, the collapsed diameters of which were 23 and 22 mm respectively. As pointed out in Section IV(*c*), these were much below the normal diameters of burst follicles.

During the ovulatory period, especially in June and July, it was not uncommon to find that two or more Graafian follicles (six in one whale) were maturing in one set of ovaries. But these cannot be regarded as potential multiple ovulations as in such a pair of ovaries there was a gradation in follicle diameter; for example, where the six maturing follicles were present the respective follicle diameters were 53, 37, 35, 34, and 30 mm. The largest follicle would probably have burst first, followed by succeeding ones if conception failed to take place.

The presence of more than one ovum in a Graafian follicle represents another possible type of multiple ovulation. A potential example of this occurring in humpback whales was found in a late foetal ovary, where one early Graafian follicle contained three ova, as shown in Plate 2.

From the present evidence, multiple ovulations in female humpback whales must be regarded as rare.

VII. DISCUSSION

An increase in paired ovary weight with increasing body length has been shown for female humpback whales, but owing to the wide range of ovary weights found just prior to and after sexual maturity (Fig. 1) there is no sharp distinction between immature and mature females on a basis of ovary weight.

Little evidence has been found of a continued increase in ovary weight with increasing age after the attainment of sexual maturity (Fig. 2), or of a decrease in ovary weight in older female humpback whales, noted by Mackintosh and Wheeler (1929) in fin and blue whales and assumed by Matthews (1937) to take place in humpback whales.

From the available material it has been found that in female humpback whales Graafian follicles up to a size of 0.13 mm in diameter are present just prior to birth. Follicles initially develop in the early years of life until from 11 to 29 mm in diameter, with a median value of 20 mm. These are the advanced but resting follicles, one (or more) of which enlarges and matures during the ovulatory period. Such resting follicles may be found in immature females close to or within the maturing length range, as well as in mature females not pregnant or lactating (see Fig. 3).

At the approach of an ovulation, one of the resting follicles enlarges to exceed 30 mm in diameter (one, apparently normal, reached 105 mm) before rupture (Fig. 3). The median diameter of very recently ruptured follicles was 37 mm, with a range of 22-60 mm, but when turgid just prior to rupture such Graafian follicles would have had greater diameters.

After ovulation the ruptured follicle rapidly develops into a corpus luteum, sometimes enclosing a translucent gel, presumably the remnants of tertiary liquor folliculi (see Brambell 1930), in the centre. A relatively rapid increase in size of the early corpus luteum over the first 2 months is indicated, growth then slowing down as the corpus luteum approaches the size range of corpora lutea of late pregnancy. Since the presence or absence of an early embryo has not been definitely established in these cases of an early corpus luteum, it is not known how far development of a corpus luteum proceeds if ovulation is not succeeded by pregnancy.

The corpus luteum (or graviditatum) initially formed early in a pregnancy remains functional throughout the gestation period. Perry (1953) recorded that in the African elephant there are accessory corpora lutea developed during the gestation period, but this does not occur in the humpback whale. There is no evidence that the corpus graviditatum in the humpback whale decreases in size toward the end of pregnancy as was suggested by Mackintosh and Wheeler (1929) in fin and blue whales. Present evidence suggests that the corpus graviditatum, after an initial rapid increase in size, continues growing (though at a much reduced rate) until pregnancy is terminated. The weights of corpora graviditata shortly before parturition (305-2185 g) cannot be related to the length of the females, the total ovarian weight, or the sex or length of the foetus, but there appears to be some relationship between the weight of the corpus graviditatum just before parturition and the relative age of the female. Figure 7 indicates that the weight of the corpus graviditatum shortly before parturition tends to be lower in younger females, rising with increasing numbers of corpora lutea in the ovaries, but is again low in relatively old females (having 30 and 38 'corpora lutea').

After parturition the resorption of the corpus graviditatum is very rapid so that by the latter part of lactation it shows no sign of its earlier activity and must be classed as a corpus albicans.

During pregnancy the Graafian follicles remaining in the ovaries diminish greatly in size, the range of largest follicles found towards the end of pregnancy being 2-18 mm in diameter, with a median value of 6 mm (Table 3). After parturition the Graafian follicles in the adult ovaries soon begin increasing in size, so that by the latter part of lactation (which on present evidence extends over approx. 10 months) the diameters of the larger follicles are again within the resting range (11-29 mm) with a median diameter of 20 mm. In a minority of cases maturation of a follicle, and even ovulation, takes place a little before the termination of lactation.

On the available evidence the ovarian cycle in mature female humpback whales (excluding those in late pregnancy or early lactation) off the Western Australian coast between June and October may be summarized as follows:

In the greater part of June, most (over 90 per cent.) of the above class of females have ovaries in the resting condition, but over 70 per cent. of these females are in late stages of lactation. In late June and early July as lactation is terminated (occasionally before), maturation of a Graafian follicle begins in the majority of these females. While mature follicles are occasionally found in June, most are found in mid July, followed by maximum numbers of ovulations in the latter half of July (Fig. 8), after which ovulation is still of common occurrence until at least early October, probably extending into November. As shown in Figure 8, most mature females not in late pregnancy or early lactation ovulate during the ovulatory period (taken as June to November), since by early October less than 15 per cent. of these females had not ovulated and showed no signs of maturing follicles.

During the normal ovulation period (between June and November) the present study shows that most (62-84 per cent.) of the ovulating females do not ovulate more than once, some twice only (16-28 per cent.) and few (up to 8 per cent.) could have ovulated three times. These proportions indicate that the mean number of ovulations for a female humpback whale during its ovulatory period is only slightly over one, probably less than 1.5.

The probability that females occasionally ovulate (with conception succeeding) at other times of the year (for example, December or January) is indicated in Section VI(*c*).

From the material examined and the conclusion that almost all mature females not in late pregnancy or early lactation ovulate between June and November, a 2-yr breeding cycle in female humpback whales can be inferred; i.e. pregnancy occupying most of the first year, lactation extending over the greater part of the second year, with ovulation following shortly after the termination of lactation, at the end of the second year.

VIII. ACKNOWLEDGMENTS

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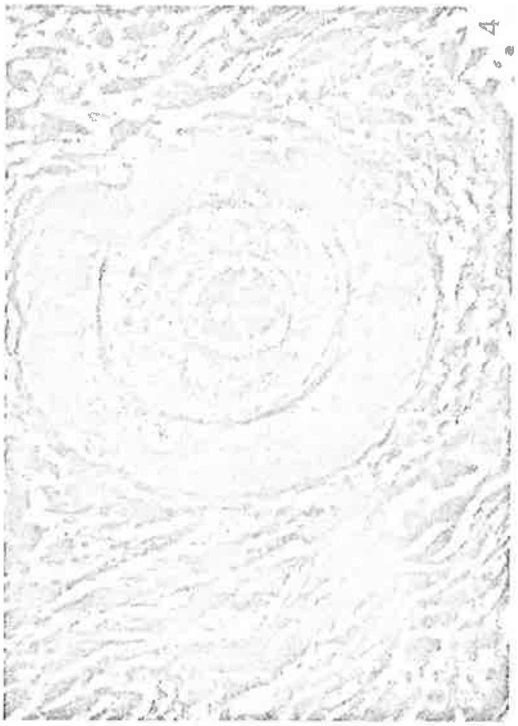
Appendix I

TOTAL LENGTH AND TOTAL OVARIAN WEIGHT

Immature Females		Resting Mature Females			
Total Length (ft)	Ovary Weight (g)	Total Length (ft)	Ovary Weight (g)	Total Length (ft)	Ovary Weight (g)
29.25	580	36.50	1045	41.83	2225
30.25	131	38.00	1480	41.92	3100
32.75	180	38.42	2230	42.08	1625
32.92	140	38.50	785	42.25	1556
33.50	208	38.75	550	42.42	1667
34.00	230	38.83	2167	42.58	965
34.33	512	39.00	1025	42·67	1105
34.58	270	39.08	720	42.67	3980
35·00	315	39.17	570	42.83	884
35.00	335	39.42	605	42.83	1185
35.08	795	39.42	1450	43.08	2129
35.08	1081	39.67	794	43.17	1050
35.17	550	39.75	650	43.17	1155
35.58	623	39.75	832	43.17	1780
35.75	640	39.92	2112	43.25	1042
36.08	511	39.92	2845	43.33	1860
36.17	255	40.00	778	43.42	3730
36.17	3425	40.08	1303	43.58	860
36.83	660	40.17	1017	43.58	1367
37.00	462	40.17	1310	43·75	1870
37.08	310	40.33	968	43.83	1845
38.00	960	40.58	2605	43.92	920
39.00	835	40.83	621	44.00	810
39.42	720	40.83	625	44.00	1470
40.50	665	40.92	907	44.25	1162
40.67	988	41.00	850	44.25	1301
40·83	1520	41.17	1466	45.00	1530
41.00	2045	41.17	1805	45.33	1825
		41.17	1969	45.42	1770
		41.17	2035	45.50	2160
		41.17	2840	45.75	1795
		41.33	3621	46.00	1310
		41.42	886	46.00	2675
		41.42	994	46.50	1776
		41.50	2305	46.50	3004
		41.58	1015	47.75	2045
		41.75	2780	49·25	2180
		41.83	1450		

OVARIES OF HUMPBACK WHALE


2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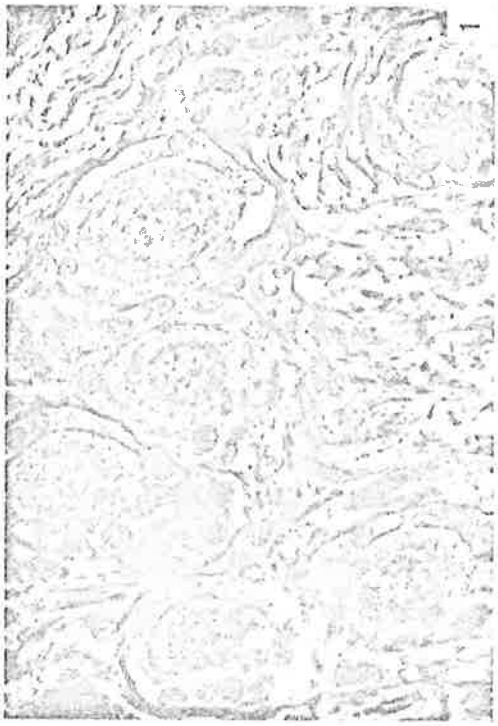
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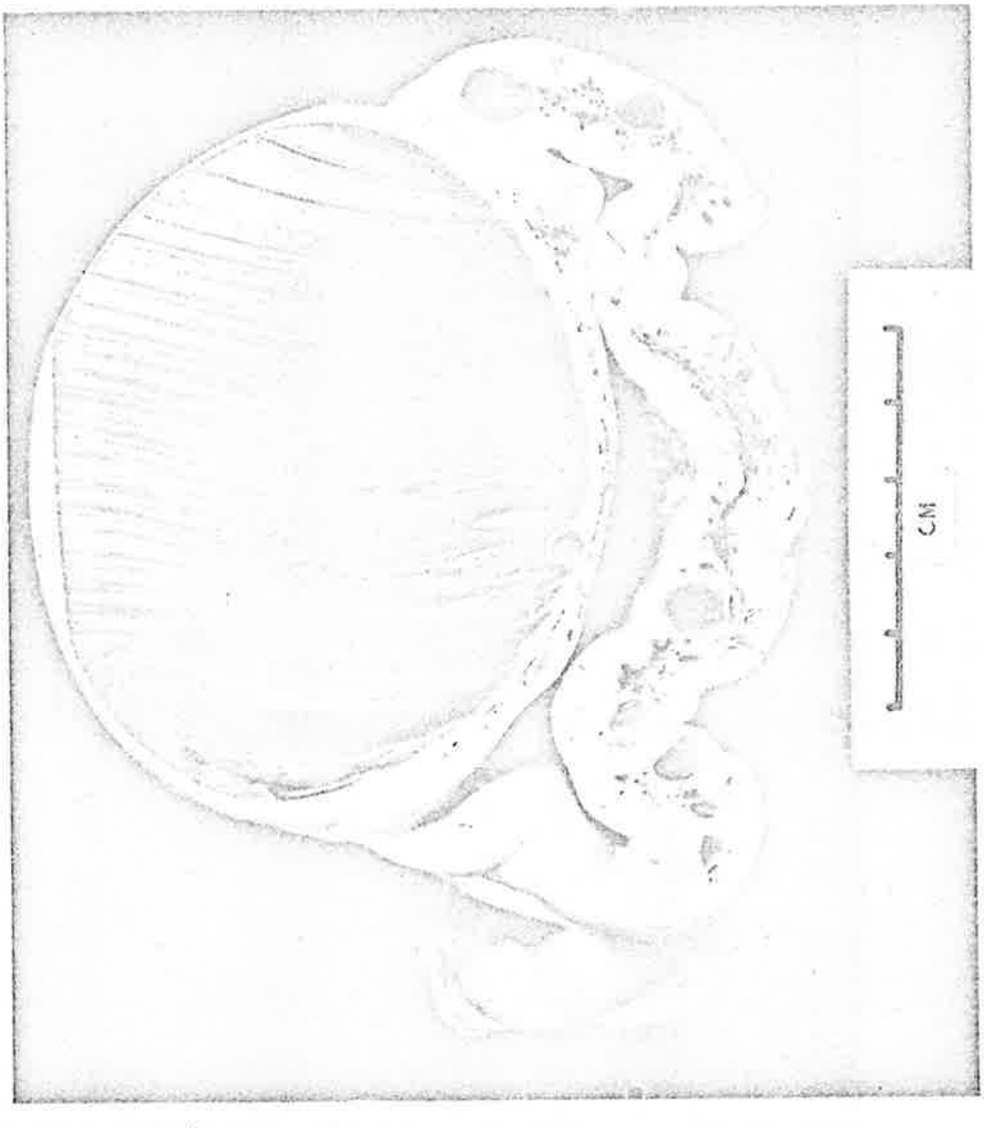
3

OVARIES OF HUMPBACK WHALE

PLATE 3

OVARIES OF HUMPBACK WHALE



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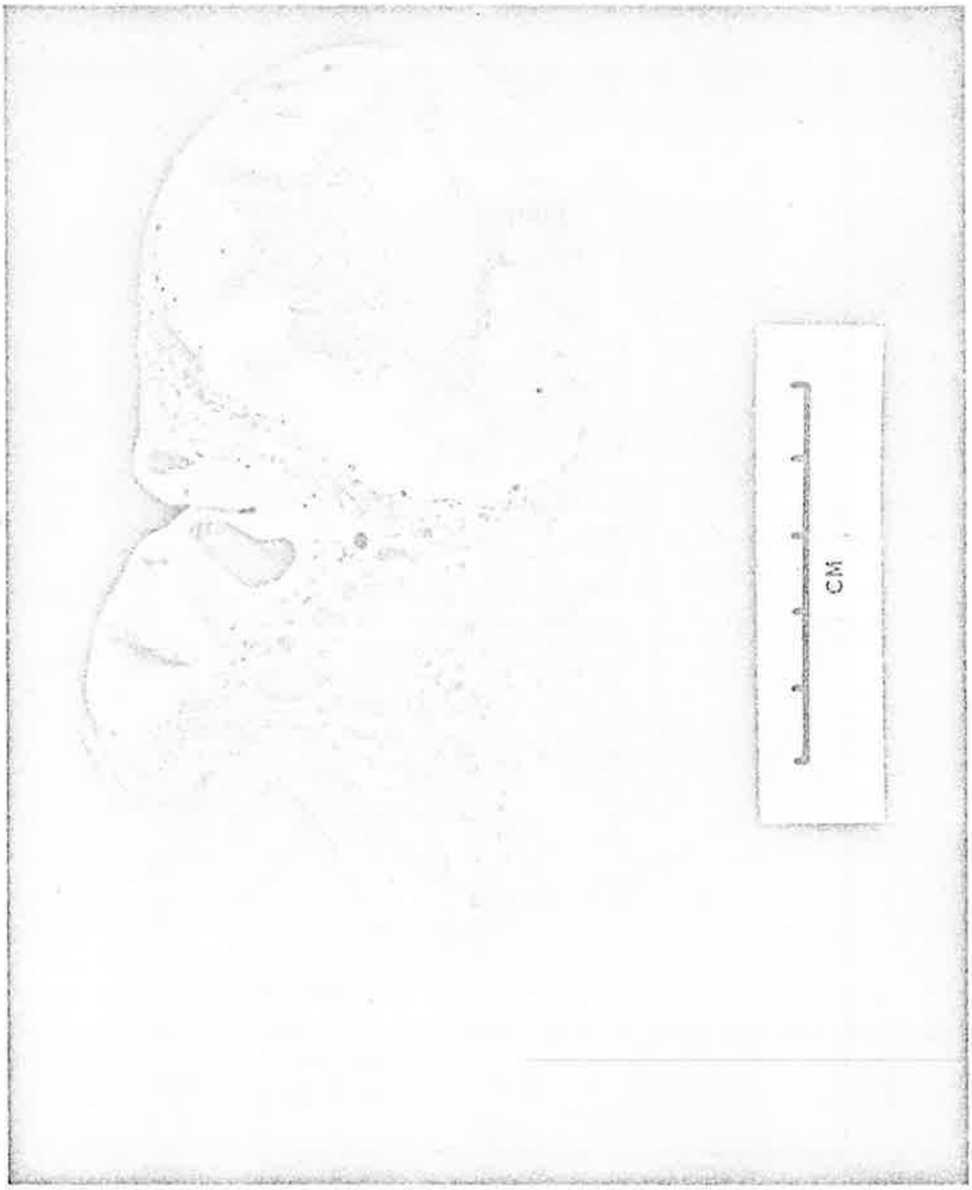
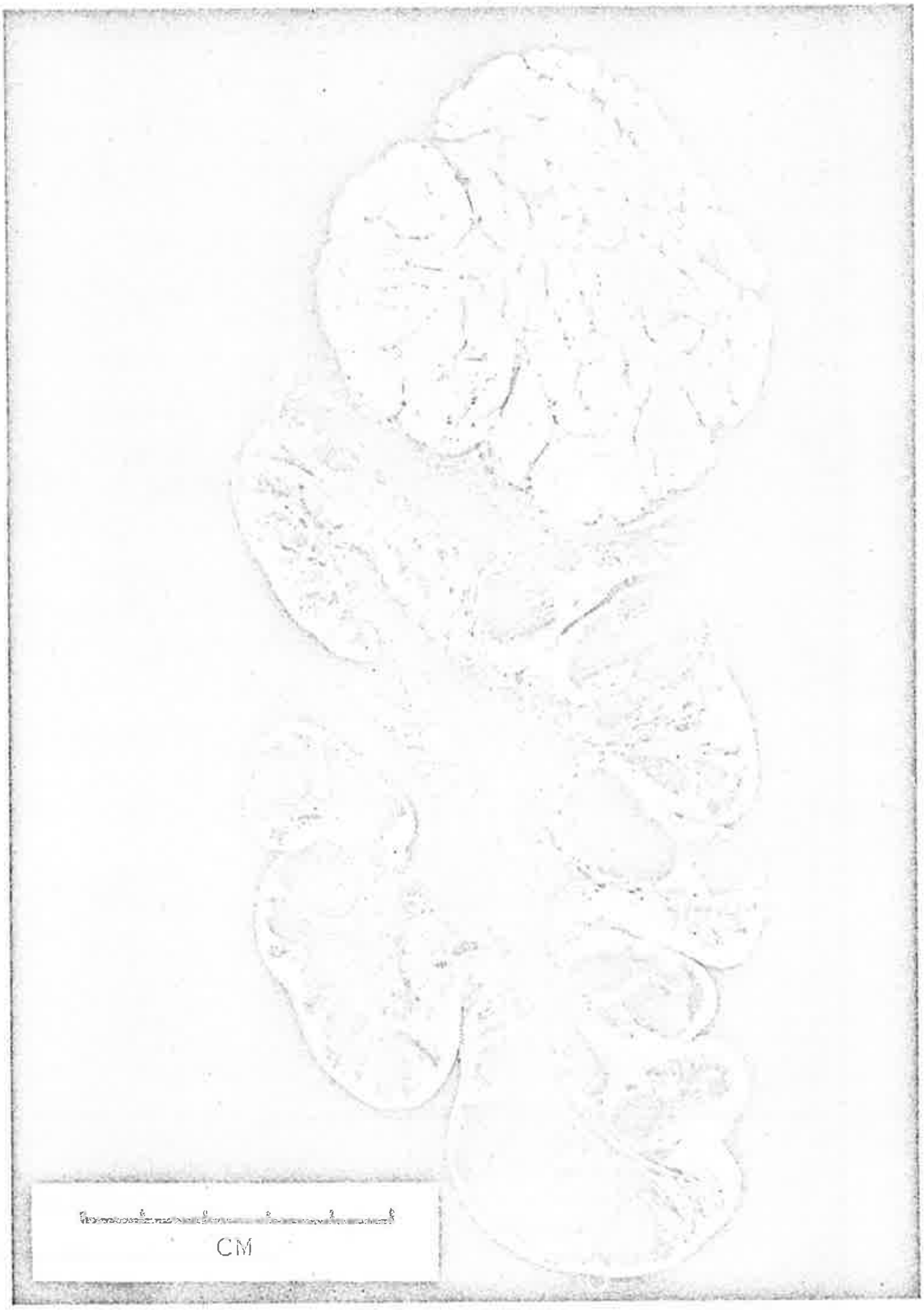


OVARIES OF HUMPBACK WHALE



OVARIES OF HUMPBACK WHALE

EXPLANATION OF PLATES 1-6

PLATE 1

Figs. 1, 2.—Primary oocytes in the ovaries of a late foetus 4.54 m (14 ft 11 in.) long. × 500.

Fig. 3.—Two early oocytes in an ovary of a late foetus 4.66 m (15 ft 3 in.) long, one oocyte containing three ova. × 500.

Fig. 4.—A well-developed oocyte from the ovaries of a late foetus 4.54 m (14 ft 11 in.) long. × 500.

PLATE 2

Above: sections through an immature ovary of a humpback whale within the maturing length range. Abundant Graafian follicles, the largest being 18 mm in diameter. Below: sections through a small ovary showing one maturing Graafian follicle 38 mm in diameter.

PLATE 3

Section of an ovary of a young female humpback whale showing a mature Graafian follicle 87 mm in diameter.

PLATE 4

Section of an ovary showing a recently burst Graafian follicle (63 mm in diameter), the lining of which is beginning to fold into the gel-filled centre to form a corpus luteum. Resting follicles to 16 mm in diameter. One corpus albicans visible.

PLATE 5

Section of an ovary showing a recently formed corpus luteum 75 mm in diameter. No embryo found in the uterus. Resting follicles to 20 mm in diameter.

PLATE 6

Section of an ovary of a female humpback whale in late pregnancy. Functional corpus luteum 125 by 115 mm with depressed scar above. Parts of three corpora albicantia visible. Graafian follicles contracted to 4 mm just visible round the edges of the section.

Paper 3

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PUBERTY, PHYSICAL MATURITY, AND RELATIVE GROWTH OF THE FEMALE HUMPBACK WHALE, *MEGAPTERA NODOSA* (BONNATERRE), ON THE WESTERN AUSTRALIAN COAST

By R. G. CHITTLEBOROUGH

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Australia

PUBERTY, PHYSICAL MATURITY, AND RELATIVE GROWTH OF THE FEMALE HUMPBACK WHALE, *MEGAPTERA NODOSA* (BONNATERRE), ON THE WESTERN AUSTRALIAN COAST

By R. G. Chittleborough*

(*Manuscript received January 24, 1955*)

Summary

At puberty the mean body length of the female humpback whales on the Western Australian coast is 38.50 ± 0.18 ft. It is demonstrated that this length gives a reliable means of calculating the proportion of sexually immature females in a series where the lengths are known. Sexual maturity (based upon the first pregnancy) may either follow immediately upon puberty or be delayed for a further year. At the approach of physical maturity (when epiphysial fusion begins) the mean body length is 45.08 ± 0.29 ft. At this stage an average of 19 ovulations have occurred. On the available material, physical maturity is reached at a mean length of 44.34 ± 0.72 ft, when close to 30 ovulations have occurred. Growth in body length of sexually mature females becomes very slow even before epiphysial fusion begins. The significance of the high number of ovulations before the attainment of physical maturity is discussed. The proportion of physically mature individuals amongst the females in recent catches off the Western Australian coast is extremely low (1.8 per cent. of 457 females examined). The lengths of male and female humpback whales at puberty, at the approach of physical maturity, and at physical maturity are compared.

I. Introduction

In research upon whales, previous authors have referred to that period when reproductive activity first commences as the attainment of "sexual maturity". Matthews (1937) considered that "sexual maturity" was reached in female humpback whales from the South Atlantic region at a body length of 12.5 m (41 ft). In the northern hemisphere, Pike (1954) referred to "sexual maturity" as being reached in female humpback whales at approximately 40 ft, but gave no data to confirm this.

In male humpback whales as discussed in a previous paper (Chittleborough 1955), puberty (when reproduction first becomes possible) and sexual maturity (when full reproductive capacity has been attained) are distinct phases separated by an interval of at least 1 year. In the present paper, puberty and sexual maturity are distinguished in the female humpback whale also and the relationship between these two phases is discussed.

There are very few previous data upon physical maturity in female humpback whales. Matthews recorded relevant information concerning five females whose vertebral epiphyses were examined. One of these females was physically mature while another was approaching this condition. In the case of fin and blue whales, much more data upon body length

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and total "corpora lutea" has been accumulated (Wheeler 1930; Laurie 1937; Brinkmann 1948; Nishiwaki and Oye 1948).

The method of examining the vertebral epiphyses for physical maturity has been previously described (Chittleborough 1955). As for male humpback whales, those females in which epiphysial fusion had begun but not extended throughout the vertebral column were classed as approaching physical maturity, while those having all epiphyses fused to their respective vertebrae were physically mature.

This material was collected at Western Australian shore-based whaling stations from 1951 to 1954, and was supplemented by some ovaries preserved by inspectors of the Western Australian Fisheries Department during 1949 and 1950. In each year the observations were made between June and October, the period during which ovulation and parturition normally occurs (Chittleborough 1954).

II. PUBERTY

It has been shown (Chittleborough 1954) that in the ovaries of the larger immature female humpbacks the Graafian follicles are numerous and well developed, the largest having a mean diameter of 20 mm. During the first pro-oestrus one of these follicles further enlarges, exceeding 30 mm in diameter and protruding considerably from the ovarian surface (Chittleborough 1954, Plates 2 and 3) before rupture and the development of the first corpus luteum. From these characteristics it is a simple matter to distinguish female humpback whales as sexually immature, at puberty, or mature.

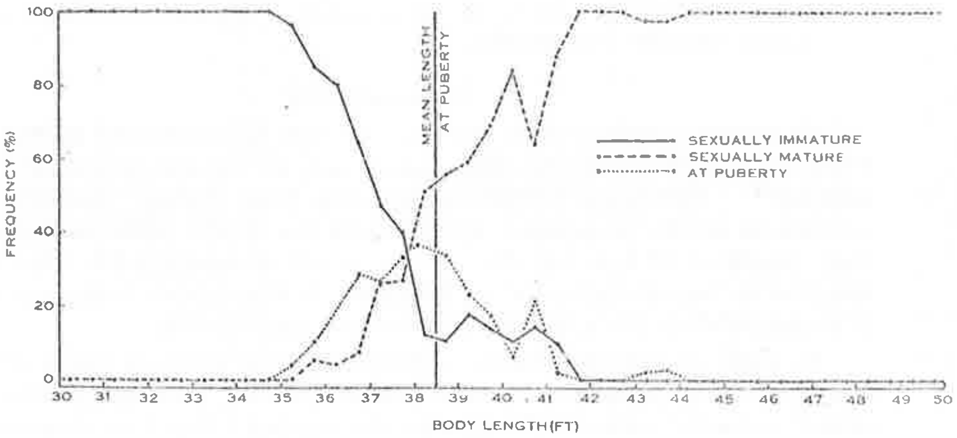

Fig. 1.—Proportions of sexually immature, pubertal, and mature females in 6-in. intervals of body length.

Of 821 females (from the Western Australian coast) whose ovaries were examined, 154 were found to be sexually immature, 77 were at puberty, and 590 were sexually mature. The distribution of these three phases within 6-in. intervals of body length are shown in Table 1 and Figure 1. The 77 females at puberty ranged from 35 ft 3 in. to 43 ft 6 in. in length, with an arithmetic mean length of 38.50 ± 0.18 ft. The median length (38.42 ft) of these females agreed closely with the mean length.

TABLE 1

PROPORTIONS OF FEMALE HUMPBACK WHALES SEXUALLY IMMATURE, AT PUBERTY, AND MATURE: WESTERN AUSTRALIAN COAST, 1951-1954

Body Length	Total Examined	Sexually Immature		At Puberty		Sexually Mature	
		No.	%	No.	%	No.	%
ft in. ft in.							
Under 34 0	11	11	100				
34 0 to 34 5	3	3	100				
34 6 to 34 11	11	11	100				
35 0 to 35 5	28	27	96.4	1	3.6		
35 6 to 35 11	20	17	85.0	2	10.0	1	5.0
36 0 to 36 5	25	20	80.0	4	16.0	1	4.0
36 6 to 36 11	14	9	64.3	4	28.6	1	7.1
37 0 to 37 5	34	16	47.1	9	26.5	9	26.4
37 6 to 37 11	15	6	40.0	5	33.3	4	26.7
38 0 to 38 5	41	5	12.2	15	36.6	21	51.2
38 6 to 38 11	28	3	10.7	10	35.7	15	53.6
39 0 to 39 5	39	7	17.9	9	23.1	23	59.0
39 6 to 39 11	36	5	13.9	6	16.7	25	69.4
40 0 to 40 5	49	5	10.2	3	6.1	41	83.7
40 6 to 40 11	28	4	14.3	6	21.4	18	64.3
41 0 to 41 5	52	5	9.6	1	1.9	46	88.5
41 6 to 41 11	32					32	100
42 0 to 42 5	50					50	100
42 6 to 42 11	34					34	100
43 0 to 43 5	46			1	2.2	45	97.8
43 6 to 43 11	41			1	2.4	40	97.6
44 0 to 44 5	41					41	100
44 6 to 44 11	22					22	100
45 0 to 45 5	38					38	100
45 6 to 45 11	21					21	100
46 0 to 46 5	19					19	100
46 6 to 46 11	15					15	100
47 0 to 47 5	9					9	100
47 6 to 47 11	5					5	100
48 0 to 48 5	7					7	100
48 6 to 48 11	1					1	100
49 0 to 49 5	3					3	100
49 6 to 49 11	1					1	100
50 0 to 50 5	1					1	100
50 6 to 50 11	0					0	—
51 0 to 51 5	0					0	—
51 6 to 51 11	1					1	100
Total	821	154		77		590	

Hence the average length at which female humpback whales reach puberty on the Western Australian coast is 38 ft 6 in. This length, as discussed below, affords a reliable method of determining the proportion of sexually immature females in a sample where only the body lengths are available.

III. SEXUAL MATURITY

In defining sexual maturity as the attainment of full reproductive capacity, Asdell (1946) pointed out that in some mammals the female produces a smaller litter from the first pregnancy than from succeeding ones, so that sexual maturity does not necessarily coincide with puberty. Since single births are the rule in the humpback whale, the females of this species must be considered as sexually mature when the first pregnancy occurs.

Some female humpback whales become pregnant at the first ovulation, so that in these females sexual maturity follows immediately upon puberty.

However, conception often does not succeed during the first ovulatory season, as shown by a number of young females whose ovaries contained one (or sometimes two) corpora albicantia while the mammary glands had not yet been active, closely resembling the glands of immature females both in size and structure. Twenty-nine females were found to be in this condition. Their lengths ranged from 36 ft 6 in. to 42 ft 6 in. with a mean value of 39.66 ± 0.31 ft. These females would probably have become pregnant for the first time during their second ovulatory season, so that sexual maturity would be reached 1 year after puberty in such cases.

IV. PHYSICAL MATURITY

(a) *Physical Maturity and Body Length*

Table 2 shows the distribution of the body lengths of 457 female humpback whales whose epiphyses were examined, the whales being classified as physically immature, approaching physical maturity, or physically mature. There is a wide range of body length within which physical maturity may be reached, the shortest physically mature female being 41 ft 8 in. long, while the epiphyses of one 49 ft 3 in. long were still unfused and another female 51 ft 10 in. long was approaching physical maturity. The proportion of physically mature females in this series is surprisingly low; this aspect is discussed below.

Table 3 lists the body lengths of those females approaching and at physical maturity. The arithmetic mean length of the 46 females approaching physical maturity is 45.08 ± 0.28 ft, which is in close agreement with the median (lying between 44.92 and 45.00 ft). The mean length of the eight physically mature females is 44.34 ± 0.72 ft. It would be expected that the mean length at physical maturity would be slightly greater than that at the approach of physical maturity (this has been demonstrated for male humpbacks (Chittleborough 1955)). The mean length of females at physical maturity would probably be slightly higher if a larger number of specimens were available.

TABLE 2

EPIPHYSIAL FUSION IN FEMALE HUMPBACK WHALES: WESTERN AUSTRALIAN COAST, 1951-1954

Body Length	Number Examined	No Epiphysial Fusion		Fusion Begun		Full Fusion	
		No.	%	No.	%	No.	%
ft in. ft in.							
Under 34 0	6	6	100				
34 0 to 34 5	3	3	100				
34 6 to 34 11	6	6	100				
35 0 to 35 5	16	16	100				
35 6 to 35 11	11	11	100				
36 0 to 36 5	12	12	100				
36 6 to 36 11	7	7	100				
37 0 to 37 5	18	18	100				
37 6 to 37 11	8	8	100				
38 0 to 38 5	26	26	100				
38 6 to 38 11	17	17	100				
39 0 to 39 5	18	18	100				
39 6 to 39 11	24	24	100				
40 0 to 40 5	24	24	100				
40 6 to 40 11	22	22	100				
41 0 to 41 5	30	30	100				
41 6 to 41 11	19	18	97.7			1	5.3
42 0 to 42 5	26	23	88.5	3	11.5	0	
42 6 to 42 11	24	22	91.7	2	8.3	0	
43 0 to 43 5	26	20	77.0	4	15.4	2	7.6
43 6 to 43 11	25	22	88.0	3	12.0	0	
44 0 to 44 5	29	19	65.5	8	27.6	2	6.9
44 6 to 44 11	11	8	72.7	3	27.3	0	
45 0 to 45 5	14	6	42.9	7	50.0	1	7.1
45 6 to 45 11	10	4	40.0	5	50.0	1	10.0
46 0 to 46 5	7	5	71.4	2	28.6	0	
46 6 to 46 11	6	4	66.7	2	33.3	0	
47 0 to 47 5	4	3	75.0	1	25.0	0	
47 6 to 47 11	3	0	0	3	100	0	
48 0 to 48 5	2	0	0	1	50.0	1	50.0
48 6 to 48 11	0	—	—	—	—	—	—
49 0 to 49 5	2	1	50.0	1	50.0	0	
49 6 to 49 11	0	—	—	—	—	—	—
50 0 to 50 5	0	—	—	—	—	—	—
50 6 to 50 11	0	—	—	—	—	—	—
51 0 to 51 5	0	—	—	—	—	—	—
51 6 to 51 11	1	0	—	1	100	0	
Total	457	403	88.2	46	10.0	8	1.8

TABLE 3

FEMALES APPROACHING AND AT PHYSICAL MATURITY

Epiphysial Fusion Begun								Full Fusion	
Body Length (ft)	Total "Corpora Lutea"	Body Length (ft)	Total "Corpora Lutea"	Body Length (ft)	Total "Corpora Lutea"	Body Length (ft)	Total "Corpora Lutea"	Body Length (ft)	Total "Corpora Lutea"
42.00	17	44.00	12	45.00	23	46.25	19	41.67	31
42.33	19	44.17	29	45.08	24	46.50	23	43.00	29
42.42	21	44.25	18	45.25	15	46.92	24	43.00	36
42.67	12	44.25	18	45.33	17	47.08	19	44.00	35
42.83	20	44.25	24	45.33	31	47.67	21	44.00	37
43.00	12	44.33	18	45.42	18	47.75	11	45.25	27
43.08	—	44.33	24	45.50	11	47.75	22	45.50	33
43.17	17	44.33	32	45.50	25	48.25	25	48.33	38
43.42	16	44.83	14	45.50	30	49.25	22		
43.58	18	44.83	22	45.58	15	51.83	23		
43.58	28	44.92	11	45.58	31				
43.75	13	45.00	19	46.00	14				

(*b*) *Physical Maturity and Total "Corpora Lutea"*

The total "corpora lutea" in the ovaries refers to the number of ovulations which have occurred, irrespective of whether represented by newly formed corpora lutea, corpora graviditata, or corpora albicantia. As discussed by Mackintosh (1942), corpora albicantia persist in the ovaries of whales, so that the total "corpora lutea" may be used as an index of relative age.

In the 46 females which were approaching physical maturity (see Table 3), the total "corpora lutea" ranged from 11 to 32 with a median value of 19, which agrees closely with the mean (19.9). From this evidence, epiphysial fusion usually begins in female humpback whales when 19 ovulations have occurred.

Figure 2 shows the body length and total "corpora lutea" of 441 females examined by the author on the Western Australian coast, indicating those physically immature, approaching physical maturity, and physically mature. Of 36 females which had ovulated 19 or more times the epiphyses had not yet begun to fuse in only three (8.3 per cent.).

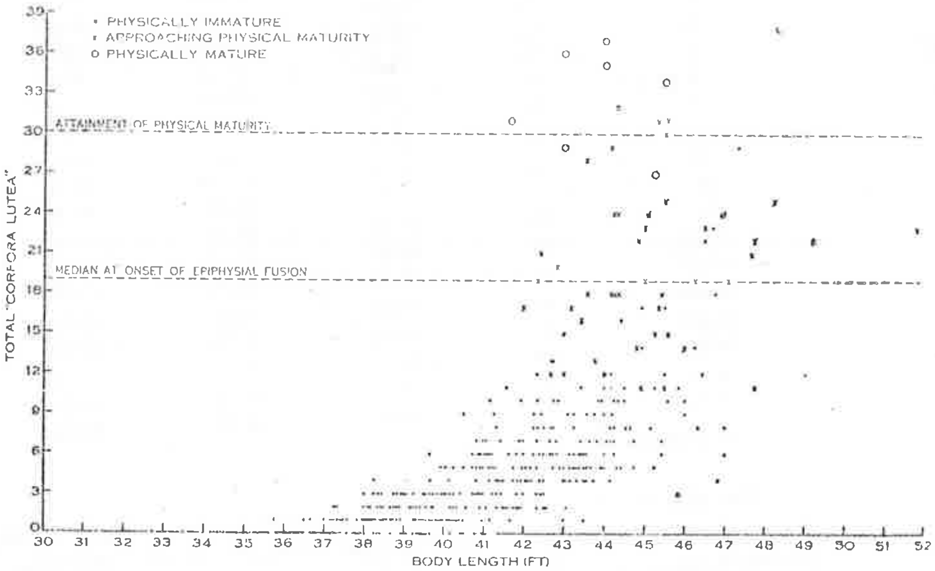

Fig. 2.—Total "corpora lutea" and physical condition (based on vertebral epiphyses) of female humpback whales taken off the western coast of Australia.

On the eight available records of physically mature females it is difficult to establish the number of "corpora lutea" which have accumulated when female humpback whales attain physical maturity. However, the distribution of the total "corpora lutea" of these eight individuals, together with those of the females approaching physical maturity (see Fig. 2), indicates that at physical maturity some 30 "corpora lutea" have accumulated in the ovaries of the female humpback whale.

V. Relative Growth Rate

It is now generally accepted (see Mackintosh 1942) that in whales the corpora albicantia persist, if not throughout life, then at least until well after physical maturity has been reached. Assuming that the ovulation rate remains relatively constant throughout life, the total "corpora lutea" in the ovaries may be used as an index of relative age in female whales.

Table 4

RELATIONSHIP BETWEEN BODY LENGTH AND RELATIVE AGE, USING NUMBERS OF OVULATIONS PRIOR TO SEASON OF KILLING AS INDEX OF RELATIVE AGE

Total Ovulations prior to Season of Killing	Number of Females	Body Length (ft)			
		Min.	Max.	Mean	Standard Deviation
0*	77	35.25	43.50	38.50	0.18
1	74	35.50	43.00	39.47	0.17
2	69	36.00	45.83	40.25	0.22
3	52	38.00	46.83	41.21	0.28
4	61	38.25	46.33	42.33	0.20
5	38	39.92	46.58	42.52	0.32
6	46	39.67	47.00	43.00	0.24
7	38	40.83	47.00	43.14	0.25
8	33	40.50	48.25	43.98	0.32
9	21	40.00	47.83	43.12	0.35
10	17	41.00	46.50	43.58	0.40
11	21	39.83	47.75	44.29	0.42
12-14	29	42.00	50.17	45.23	0.39
15-17	17	42.00	49.00	45.37	0.43
18-20	21	41.00	47.08	44.79	0.38
21-23	17	41.83	51.83	46.50	0.58
24-26	16	43.67	48.25	45.49	0.32
28-30	10	43.00	48.75	45.51	0.65
31-38	7	43.00	48.33	44.96	0.66

* At puberty.

On the Western Australian coast, female humpback whales are killed from June to October, the period during which oestrous cycles and parturition occur. This means that some females are taken shortly after ovulation (so that a newly formed corpus luteum is present), while others are killed during pro-oestrus. In order to apply a uniform standard of relative age, any ovulations which occurred just prior to killing must be omitted. Hence as an index of relative age the author has used the total number of ovulations which had occurred in seasons prior to that in which the whale was killed. These ovulations may be represented either by corpora albicantia alone, or in females in very advanced pregnancy would include the corpus graviditatum, as this would represent an ovulation in the previous season.

Table 4 shows the ranges and mean lengths of 587 sexually mature females, grouped according to the number of ovulations which had occurred prior to the season of killing, and also the range and mean length of 77 females killed at puberty (representing group 0, as these had not ovulated in previous seasons). The mean length of each group is shown against the number of previous ovulations in Figure 3.

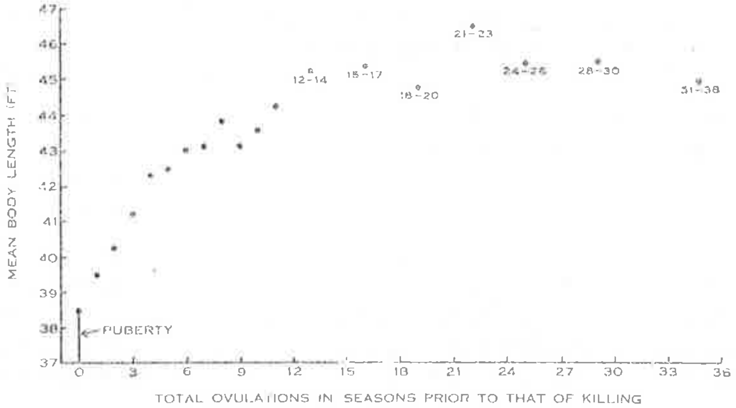

Fig. 3.—Growth curve for female humpback whales from the Western Australian coast, using as an index of relative age the total ovulations in seasons prior to that of killing.

Using the number of previous ovulations as an index of relative age, the mean lengths in Figure 3 indicate the growth curve of sexually mature female humpback whales in the stock fished off the Western Australian coast. The mean length is shown to increase with relative age at a decreasing rate until the curve approaches a horizontal line. This curve shows that growth in length has almost ceased long before physical maturity (based on full epiphysial fusion) has been reached (at approximately 30 ovulations). The apparent slight drop in the mean length of relatively old females (31-38 previous ovulations) is probably due to the small number of these females which were found, rather than to a real decrease in length as females aged.

No such relative growth curves are available for female humpback whales taken in other regions, but that given in Table 4 and Figure 3 might be used in a comparison of the growth of female humpback whales from different areas. Using this method, Pike (1953) has clearly demonstrated that the growth of female fin whales from the northern hemisphere is much slower than that of those from the southern hemisphere.

VI. Discussion

While the mean length of female humpback whales at puberty is 38 ft 6 in., the recorded range is very wide (35 ft 3 in. to 43 ft 6 in.). As previously discussed (Chittleborough 1954) this might be the result of some females reaching puberty when 2 years of age and others at 3 years.

The distribution of the body lengths of the 77 females at puberty has been analysed in this regard, but the data are incapable of supporting this hypothesis. It is still possible that puberty is not reached until the third year in some females, but the variable individual growth rates prevent this being demonstrated in the available material.

It was stated earlier that the mean length of female humpback whales at puberty (38 ft 6 in.) can be used to determine the proportion of sexually immature females in a sample where only the body lengths are known. As a test of the reliability of this method, the 821 females whose ovaries have already been examined may be used. It was found that 200 (24.4 per cent.) of these were under 38 ft 6 in. in length, in close agreement with 188 (22.9 per cent.) which had not yet ovulated.

Sexual maturity (based on the first pregnancy) may either follow immediately upon puberty, or be delayed for a further year, the females then having an average length of 39.66 ± 0.31 ft. Because these two classes of females exist, it is not possible to indicate a single mean length of female humpback whales on reaching sexual maturity.

The rate of growth, initially relatively rapid, has so declined before epiphysial fusion commences that there is no significant difference in length between those females approaching and those having attained physical maturity, while many females within the length ranges of these stages are still physically immature, as shown by Figure 2.

Ovulation, on the other hand, continues in these older females, presumably at a rate similar to that in younger females. No evidence of a climacteric has been found in physically mature female humpback whales taken on the Western Australian coast. In several cases the ovaries carried large thin-walled cysts (Chittleborough 1954), probably degenerate follicles, but normal follicles were also present and ovulation had recently occurred in three of these females.

At physical maturity in the female humpback whale the ovaries have accumulated some 30 "corpora lutea". This is surprisingly high when compared with the corresponding findings in fin and blue whales shown in Table 5.

Assuming that comparable techniques were used for the determination of total "corpora lutea", the greater accumulation of "corpora lutea" in physically mature humpback females might be interpreted as indicating a higher frequency of ovulation in this species than in fin and blue whales. But it has been shown (Chittleborough 1954), that the number of ovulations occurring in one ovulatory period (June to October) is probably a little lower in humpbacks than that estimated by Peters (1939) for one ovulatory period (in a 2-year breeding cycle) of fin and blue whales. In fin and blue whales there is a lactation anoestrus so that ovulation occurs every second year. If a post partum ovulation regularly occurred in female humpback whales, the rate of accumulation of corpora albicantia would be double that in fin and blue whales, thus accounting for the higher number of "corpora lutea" in physically mature humpback whales (approximately double that of physically mature fin and blue whales).

TABLE 5

TOTAL "CORPORA LUTEA" IN FIN AND BLUE WHALES AT PHYSICAL MATURITY

Author	Fin Whales	Blue Whales
Wheeler (1930)	15	—
Laurie (1937)	—	11
Peters (1939)	14-15	12
Nishiwaki and Oye (1948)	14	12
Brinkmann (1948)	13	11-12

Although very convenient, there is not a great deal of evidence to support this hypothesis. A lactating female humpback suckling a very young calf (both taken recently by special permission for research purposes) was found to have ovulated shortly after parturition, and two other females were found to be in advanced pregnancy and yet in late stages of lactation. Hence post partum oestrus can occur in female humpback whales, but at present there is little indication that it is a regular feature in this species. The remaining conclusion accounting for the high number of "corpora lutea" in the ovaries of physically mature female humpback whales is that physical maturity is attained relatively later in the life of humpback whales than in fin and blue whales.

When taking whales the gunners select the larger individuals, yet in the representative series examined for physical maturity (Table 2), only 1.8 per cent. (eight in a total of 457) of the females had reached physical maturity. The proportion of physically mature males was similarly low, viz. 1.4 per cent. of 567 examined (Chittleborough 1955). Wheeler (1930) suggested that the proportions of physically mature whales might be a very useful index of the condition of the stock. However, in the humpback whale comparable records from past whaling ventures on the Western Australian stock are not available. Brinkmann (1948) found that 37.4 per cent. of 561 female fin whales and 22.4 per cent. of 295 female blue whales, taken in Antarctic areas II to IV in 1939-40, were physically mature. Similar proportions of physically mature female fin and blue whales have been reported by Wheeler (1930) and Laurie (1937).

As suggested for male humpback whales (Chittleborough 1955), the very low proportions of physically mature individuals in recent catches from the Western Australian coast might be due to:

(i) a migratory difference—physically mature individuals moving further offshore or not all leaving the Antarctic each autumn;

(ii) a species difference—epiphysial fusion occurring in humpback whales later in life than in other species of whales;

(iii) a fishing effect—previous heavy fishing with a strong selectivity towards larger individuals resulting in the removal of many physically mature individuals from the stock.

There is no evidence that the first possibility applies in this species but the much lower proportion of physically mature individuals in this than in other species of whales might be due in part to the already suggested later age at which humpback whales reach physical maturity. The very low percentages of physically mature humpback whales in recent catches off this coast might also be the result of previous heavy fishing upon this stock. Evidence of such changes within this stock is accumulating and will be considered in a later paper.

From the results of the investigation on the Western Australian coast, the lengths of male and female humpback whales from this stock can be compared at puberty and at the approach and attainment of physical maturity. These lengths are summarized in Table 6.

Table 6

LENGTHS OF MALE AND FEMALE HUMPBACK WHALES AT PUBERTY AND PHYSICAL MATURITY

Condition	Minimum		Maximum		Mean (ft)
	ft	in.	ft	in.	
Puberty:					
Males	33	4	40	10	36.75
Females	35	3	43	6	38.50 ± 0.18
Approaching physical maturity:					
Males	38	10	45	10	41.90 ± 0.17
Females	42	0	51	10	45.08 ± 0.29
Physical maturity:					
Males	39	10	45	6	42.97 ± 0.67
Females	41	8	48	4	44.34 ± 0.72

At all three phases the minimum, maximum, and mean body lengths of the females are greater than those of the males. The mean length of the females approaching physical maturity is significantly higher than that of the males at this stage ($t = 10.11$ on 124 degrees of freedom). The test of significance upon the females and males which had reached physical maturity was inconclusive ($t = 1.39$ on 14 degrees of freedom), no doubt owing to the small number of records of this stage at present available. It has long been known that female humpback whales grow faster, attaining greater lengths than the males, but the values in Table 6 indicate the degree to which this occurs.

VII. Acknowledgments

The cooperation of the Norwest Whaling Company and the Australian Whaling Commission, enabling material to be collected from their respective stations at Point Cloates and Carnarvon, is gratefully acknowledged.

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Paper 4

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THE BREEDING CYCLE OF THE FEMALE HUMPBACK WHALE, *MEGAPTERA NODOSA* (BONNATERRE)

By R. G. Chittleborough

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Australia

THE BREEDING CYCLE OF THE FEMALE HUMPBACK WHALE, *MEGAPTERA NODOSA* (BONNATERRE)

By R. G. Chittleborough*

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Summary

The gestation period in the humpback whale is of almost 12 months' duration, most conceptions occurring early in August with parturition at the beginning of the following August. The modal length of calves at birth is 14 ft. The sex ratio at birth is 51·4 per cent. males to 48·6 per cent. females. Twin foetuses are occasionally recorded. There is no preference towards either right or left ovary or uterine cornu with regard to ovulation or pregnancy. The breaking of the umbilical cord at birth is described.

The histological appearances of the mammary gland during advanced pregnancy and during lactation are described and illustrated. Upon the evidence presented it is concluded that lactation in this species extends over 10½ months, suckling generally commencing in mid August and terminating at the end of the following June. The composition of the milk has been determined during various stages of lactation.

Oestrous cycles rarely occur during pregnancy, but examples of ovulation following shortly after parturition, while the females are suckling their calves, are cited. It is shown that when the calf is lost at or soon after birth, oestrous cycles usually recommence at once. Where the calf is suckled for the normal period (10½ months) there is no anoestrous period following the end of lactation as oestrous cycles recommence in July, immediately after (occasionally just before) weaning at the end of June.

Three types of breeding cycle are shown for the humpback whale. In the most common cycle, absence of the post-partum ovulation, or its occurrence without conception, results in one calf in 2 years. On the other hand, a successful post-partum ovulation results in two calves in 2 years. In the third type of cycle, loss of the first calf at or just after parturition is balanced by a second pregnancy succeeding immediately afterwards. This results in two pregnancies in 2 years with only one calf reared.

I. INTRODUCTION

Southern humpback whales feed during the summer in Antarctic waters and migrate northwards each autumn to spend the winter months in tropical and subtropical regions (Matthews 1937; Mackintosh 1942). It is probable that most, if not all, individuals take part in this seasonal migration. Australian coastal whaling stations take fixed quotas of these whales between June and October, while in the Antarctic the catching of humpback whales is at present permitted during the first 4 days of February.

Owing to their size and habits it is not possible to make repeated observations upon individual humpback whales in order to determine the length of the gestation period and the duration of lactation. To establish the times of occurrence and duration of these phases one must obtain evidence from a large number of individuals killed at varying stages and then decide the most probable normal sequence of events in the species.

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The only real attempt to do this for humpback whales was that of Matthews (1937), who suggested that gestation occupied about 11 months, most conceptions occurring in September with parturition the following August. The body length at birth was considered to lie between 4·5 and 5·0 metres (14 ft 9 in. to 16 ft 5 in.). On the very limited evidence available, Matthews proposed that the calf was suckled for approximately 5 months. A breeding cycle of one calf in 2 years was given for this species, the majority of the first year being occupied by pregnancy, the first 5 months of the second year in lactation, and the remaining 7 months in non-lactating anoestrus. It was suggested that in a few females ovulation might occur at the end of the 5 months' lactation, so that in some cases two pregnancies would occur in 3 years.

From the material collected in recent years (1949–1955) at shore-based whaling stations on the west coast of Australia, these findings may now be reviewed and extended.

II. Material

The results given in this paper are based primarily upon 390 sexually mature female humpback whales examined in detail by the author. Further valuable information was obtained from the ovaries collected by whaling inspectors from 287 mature females. These females were sampled at random from the normal catches at Western Australian whaling stations. In addition, three females and their calves were killed under special licence for research purposes and fully examined by the author.

Certain aspects of the results obtained from these whales have already been published (Chittleborough 1954, 1955).

In this paper the records kept by whaling inspectors of all foetuses found (at Western Australian whaling stations) between 1949 and 1955, have been examined for certain aspects of pregnancy and parturition. Also with reference to parturition, the results of aerial observations upon 1765 adult humpback whales have been used. An account of some of these aerial observations has already been published (Chittleborough 1953).

Records of foetuses from Antarctic areas IV and V (from 1949 to 1956) (see Mackintosh (1942) for definition of areas) were obtained from catch returns supplied by International Whaling Statistics, Sandefjord, Norway.

Material from mammary glands for histological examination was fixed in Heidenhain's Susa fixative, and paraffin sections were cut at 7 μ and stained with haematoxylin and eosin. As a rule a sample from the centre of the mammary gland was taken to represent the condition of the whole gland, but in several cases anterior, central, and posterior samples were taken and compared.

Samples of milk from 15 females in progressive stages during and at the end of lactation were taken in bottles of 110 ml capacity, after two drops of commercial formalin (40 per cent. formaldehyde) had been placed in each bottle. The samples were stored in a refrigerator (without freezing) until analysed by the Government Chemical Laboratories of Western Australia.

III. PREGNANCY

(a) *Gestation Period*

Early embryos are seldom recorded; since 1949 only two have been obtained from females taken on the west coast of Australia. One small specimen (damaged) was found on September 4, and another on September 8 (crown–rump length 11 mm). Because of the paucity of early embryonic stages, the time of ovulation is considered as an index of the time of conception.

TABLE 1

HUMPBACK FOETUSES FROM ANTARCTIC AREAS IV AND V, 1949–1956: LENGTH FREQUENCY DISTRIBUTION

Foetal Length (ft)		Number of Foetuses Recorded						
	Year:	1949–50	1951	1952	1953	1954	1955	1956
	Catching Period:	Dec. 16 to Jan. 5	Feb. 2–8	Feb. 1–5	Feb. 1–4, 16–18	Feb. 1–4	Feb. 1–4	Feb. 1–4
0·5		2	1			1		
1		80	19	18		6	5	26
1·5		44	2	4	2	5		6
2		127	71	46	13	12	11	59
2·5		24		4		8	18	8
3		29	115	65	37	18	27	62
3·5		2	3	2	7	11	19	17
4		1	103	55	42	14	21	52
4·5					4	2	4	5
5			35	7	25	1	9	6
5·5						1		1
6		2	2	4	4		9	1
7		1					1	
8		1					2	
11			1					
Mean length (ft):		1·9	3·2	3·0	3·7	2·9	3·5	2·8

In a previous paper (Chittleborough 1954) it was shown that: (1) ovulation in the female humpback whale may occur from the beginning of June until early October; (2) most females (approximately 70 per cent.) ovulate only once during this period; (3) most ovulations occur in the latter part of July and early in August (Fig. 8 of the above paper). From these facts it may be deduced that on the west coast of Australia most pregnancies commence early in August. A number of females may become pregnant later in August or in September, either from a second ovulation or in some cases as a result of a first ovulation which was slightly later than usual.

In catches from Antarctic waters during the southern summer, high proportions of pregnant females are taken. Table 1 shows the length frequency distribution of 1452 foetuses recorded from Antarctic areas IV and V from 1949 to 1956.

When pregnant females return to the Australian coast in the following winter, they are generally in more advanced stages of pregnancy. From 1949 to 1955, 250 foetuses have been recorded from catches on the west coast of Australia. Figure 1 shows the length and date of killing of each foetus, and the length frequency distribution. With one exception (discussed later) these foetuses were close to term.

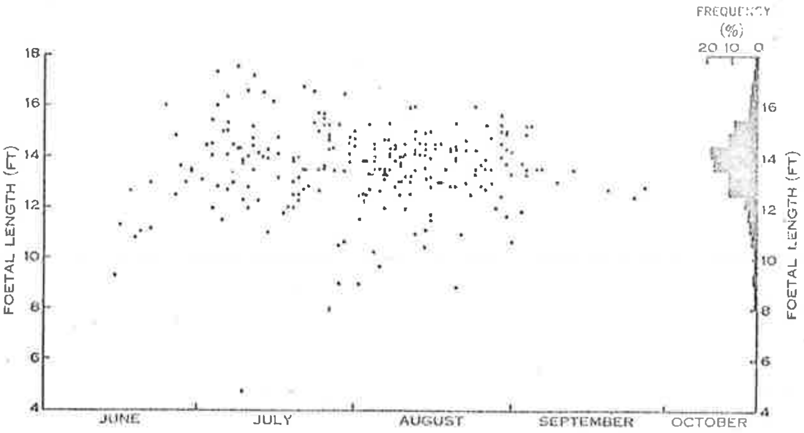

Fig. 1.—Foetal lengths and length frequency distribution of foetuses from the Western Australian coast, 1949–1955.

Figure 2(*a*) shows the distribution of these near-term foetuses as recorded throughout the catching period (June–October). Very few are recorded during June, in spite of high proportions of sexually mature females in the catches for that month.

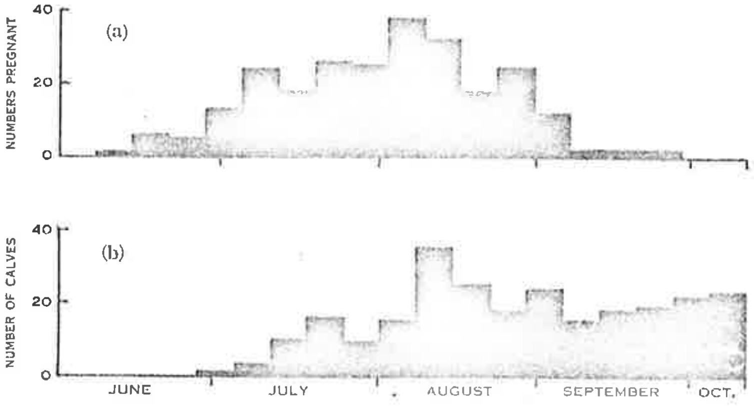

Fig. 2.—(*a*) Distribution of 249 females in advanced pregnancy taken on the Western Australian coast between June and October from 1949 to 1955. (*b*) Distribution of 253 new-born calves sighted amongst 1765 adult humpback whales observed from the air off Point Cloates during 1952 and 1953.

This indicates that females in advanced pregnancy are relatively late in reaching this coast during the northward migration. Figure 2(*a*) shows that females in advanced pregnancy are of most frequent occurrence (off this coast) during July and early

August, but that numbers fall from mid August, apparently as increasing numbers of births occur.

Another approach to the time of parturition is by recording the presence of new-born calves observed amongst the adults moving along the coast. Aerial observations of this kind were made in the region of Point Cloates in 1952 and 1953. A total of 1765 adult humpback whales were checked (from the air), and 253 new-born calves were recorded. The weekly occurrence of the calves throughout the catching period is shown in Figure 2(*b*). This indicates that the first calves are born towards the end of June, slightly more in July, and maximum numbers in August.

By comparing the distribution of near-term foetuses (Fig. 2(*a*)) with that of new-born calves (Fig. 2(*b*)), it can be said that in the humpback whale parturition occurs on the west coast of Australia between June and October, but with a maximum frequency early in August.

From the available data upon ovulation and parturition, as discussed above, the average length of the gestation period in this species is close to 12 months, both conception and parturition occurring with maximum frequency early in August.

(*b*) *Length of Calf at Birth*

Since calves are protected by law it is seldom possible to obtain the length at birth from direct observations. One new-born calf, taken on August 3, 1955, was 15 ft 3 in. in length. From the condition of the uterus of the cow and the unhealed umbilicus of the calf, parturition had taken place approximately 1 week earlier.

The mean length of 249 near-term foetuses taken on the west coast of Australia was 13 ft 8 in. However, this must be slightly below the mean length at birth since at least some of these foetuses would have increased in length in the short time remaining before parturition. The lengths of near-term foetuses shown in Figure 1 are of almost normal distribution round a modal length of 14 ft. This indicates that the size at parturition is normally distributed round that length. From the material examined there does not appear to be any difference between the lengths of males and females at birth.

(*c*) *Foetal Sex Ratio*

Of 249 near-term foetuses taken on the west coast of Australia from 1949 to 1955, 51·4 per cent. were males. From the Antarctic (roughly at mid pregnancy) 1448 humpback foetuses were sexed in catches from areas IV and V between 1949 and 1956; 51·9 per cent. of these foetuses were males.

(*d*) *Multiple Pregnancies*

Multiple pregnancies have occasionally been recorded in the humpback whale (Matthews 1937). Of 1449 pregnant humpback whales listed in the International Whaling Statistics from Antarctic areas IV and V in seasons 1949–50 to 1955–56, only four cases (0·28 per cent.) of twinning were recorded. Since 1949 only one multiple pregnancy (twin female foetuses) has been recorded from humpback whales taken on the Australian coast. Two examples of multiple ovulations have been described (Chittleborough 1954).

(e) *Prevalence of Ovulation and Pregnancy on a Particular Side of the Body*

In some whales taken off the west coast of Australia, ovulations had been predominantly from one ovary, the right in some individuals and the left in others. However, in 148 sexually mature females, a total of 613 ovulations had occurred from the left ovary and 655 from the right. This distribution does not differ significantly from a random one. In 22 pregnant females the 22 corpora graviditata were equally distributed between right and left ovaries, and implantation had always occurred on the same side as the ovulation.

(*f*) *Breaking of the Umbilical Cord*

In the near-term foetus the normal skin on the ventral surface of the body extends up to 7 in. along the umbilical cord, covering the cord in this region. On several occasions when a near-term foetus slid from the uterus during cutting operations, the pulling of the foetus against the placenta caused the umbilical cord to break. In each case the break occurred cleanly against the body wall, so that all that remained attached to the foetus was an empty tube of the skin which had previously enveloped the base of the cord. The same condition was found in a new-born calf. It is probable that the cord normally breaks here during parturition. Van Utrecht (personal communication) has made similar observations upon new-born young of the white-sided dolphin (*Lagenorhynchus acutus* (Gray)).

(*g*) *Mammary Glands During Advanced Pregnancy*

In pregnant females close to parturition the lobules and alveoli of the mammary glands are well developed and in most cases fluid is present in the ducts. This is often a clear liquid, slightly yellow or pale brown in colour, or sometimes turbid and white, looking like much diluted milk. Large quantities may be present at this stage, the fluid often spurting from the nipples as the pregnant female is hauled from the water.

Histologically two phases could be distinguished in the mammary glands of pregnant females close to parturition. One phase (see Plate 1, Fig. 1) was characterized by the large vesicular nuclei of the alveolar cells, the cytoplasm of which stained very little (with haematoxylin or eosin). These cells showed little sign of secretory activity. The lumina of the alveoli were generally empty, except that scattered alveoli contained a non-granular acidophilic secretion, which was also present in some ducts. This fluid may be similar to the globulin secretion produced in the mammary glands from mid pregnancy in goats (Drummond-Robinson and Asdell 1926).

In the second phase (see Plate 1, Fig. 2) the nuclei of the alveolar cells were generally slightly smaller, non-spherical, and darker-staining with more concentrated chromatin. The cytoplasm was more granular and basophilic, while occasional clear droplets in the cytoplasm suggested that globules of fat (removed during the preparation of sections) were being secreted. Within the alveoli there was abundant granular basophilic material with a few fat globules. Secretory activity was greater in peripheral alveoli within each lobule.

It would appear that these two phases follow each other in the order given above, the second phase approaching the histological appearance of the mammary glands of actively lactating females. The second phase is probably reached very shortly before parturition. If this is so, one foetus 12 ft 7 in. long was very close to term.

IV. LACTATION

(a) *Characteristics*

As pointed out by van Lennep and van Utrecht (1953) there is considerable confusion regarding the characteristics and definition of lactation in whales. In its true sense a lactating female is suckling a calf, but once the whale is on the flensing deck it is difficult to establish positively that a female whose mammary glands are milk-filled had in fact been accompanied by a suckling calf up to the time of killing.

In the present work the first criterion of lactation was the presence of apparently normal milk. Other fluids—for example, the less dense and often discoloured liquid as often found in the mammary ducts during advanced pregnancy, or the rather white watery fluid found in some glands involuting after lactation—were not classed as milk. The quantity of normal milk is of little diagnostic value. Soon after parturition the calf may be feeding frequently, so that a female killed early in lactation might not be carrying much milk in the ducts although lactating heavily. This was found in one case (discussed later) where a female and its young calf were taken. On the other hand during the weaning period the calf may suckle less regularly, so that milk may accumulate in the mammary glands, even to the extent that it is forced from the nipples as a female in late lactation is hauled from the water. Also if the calf is lost the milk would temporarily accumulate in the female's mammary glands. Accordingly the presence of large quantities of milk is not necessarily proof that a suckling calf was present when the female was killed.

As a second criterion of lactation the histological appearance of the mammary glands was considered. It has been shown in the guinea-pig (Hesselberg and Loeb 1937) and the mouse (Williams 1942) that some involutional changes begin in the mammary glands shortly before weaning, apparently as a result of lessened suckling. Thus if the mammary glands are actively secreting and show no signs of involution, the young are still suckling. This interpretation was followed with those humpback whales whose mammary glands contained apparently normal milk. If the alveoli of the glands showed no sign of involution and the cells lining the alveoli were actually secreting, the female was classified as still suckling the calf. If the ducts contained milk and the alveolar cells were no longer secreting (generally with signs of resorption of the alveolar cells) it was considered that the female had either recently lost, was weaning, or had just finished weaning the calf, and that the apparently normal milk present in the ducts was a residuum which would have shortly disappeared.

In several cases where milk was present, samples of mammary gland tissue from anterior, central, and posterior regions of the glands were preserved in order to compare the activity of the various regions. The condition of the lobules was generally found to be uniform throughout the gland, although in one female killed at the end of lactation, involution of the lobules in the posterior region of the mammary gland appeared to be slightly in advance of that of lobules in the anterior part of the gland.

The condition of the ovaries gives some indication of how recently parturition has occurred. Soon after parturition the corpus luteum of pregnancy is still large and, though involuting, shows evidence of its recent activity (see Plate 2). Towards the end of the suckling period the resorption of the recently functional corpus luteum is so far advanced that it must be classed as a corpus albicans, and is often reduced to such an extent that it is difficult to decide which corpus albicans had been functional most recently (Chittleborough 1954).

If parturition has only recently occurred the uterus may still be somewhat enlarged, with a thickened fibrous wall and low pointed glandular folds in the endometrium. However, after parturition the uterus usually returns rapidly to a similar size and structure as before the pregnancy, so that the condition of the uterus is a useful diagnostic feature for only a brief period after parturition.

(*b*) *Duration of Lactation*

Since in most cases parturition takes place early in August (Section III(*a*)), it is suggested that most females have begun lactating by mid August.

TABLE 2

FEMALES WITH MILK BUT SHOWING NO EVIDENCE OF RECENT PARTURITION: INCIDENCE AMONGST 348 SEXUALLY MATURE FEMALES TAKEN ON THE WESTERN AUSTRALIAN COAST (1949–1955)

Ten-day Period	Total Mature Females Examined	Females with Milk but No Evidence of Recent Parturition	
	No.	No.	Percentage
June 1–10	26	19	73·1
June 11–20	64	48	75·0
June 21–30	31	24	77·4
July 1–10	20	6	30·0
July 11–20	35	8	22·9
July 21–30	16	1	6·3
July 31–Aug. 9	41	3	7·3
Aug. 10–19	18	1	5·6
Aug. 20–29	23	0	0·0
Aug. 30–Sept. 8	35	2	5·7
Sept. 9–18	21	2	9·5
Sept. 19–28	10	1	10·0
Sept. 29–Oct. 8	8	1	12·5

Regarding the termination of lactation, it has been found that many sexually mature, non-pregnant females taken on the west coast of Australia in June and early July of each year carry milk in the mammary glands (Chittleborough 1954). The ovaries and uteri of these females were generally in a resting (anoestrous) condition, indicating that the previous birth had occurred some months before. In a few cases a Graafian follicle was maturing, or ovulation had recently occurred.

Table 2 and Figure 3 show the percentages of females whose mammary glands contained normal milk and which showed no sign of a recent birth, amongst sexually mature, non-pregnant females taken in each 10-day period from June to October. Figure 3 indicates that most mature, non-pregnant females are lactating in June, but that lactation usually ceases by the beginning of July.

However, as stressed in the previous section, the presence of milk is not proof in itself that a calf is being suckled, but the cytological condition of the mammary glands affords some confirmatory evidence that suckling is proceeding. Many of these females in milk had been dead too long to allow a satisfactory histological examination. The mammary glands were sectioned in 22 specimens of freshly killed females whose glands contained milk but which showed no evidence of a recent birth. The glands of 17 of these, all killed during June and the first week of July, were fully developed and secreting, having the same microscopic appearance as the glands during early lactation (compare Figs. 1 and 2 of Plate 3). The mammary glands of the remaining five, all killed after the first week of July, were regressing and cells lining the alveoli were no longer secretory (see Plate 4, Fig. 1). This suggests that these females had recently weaned their calves.

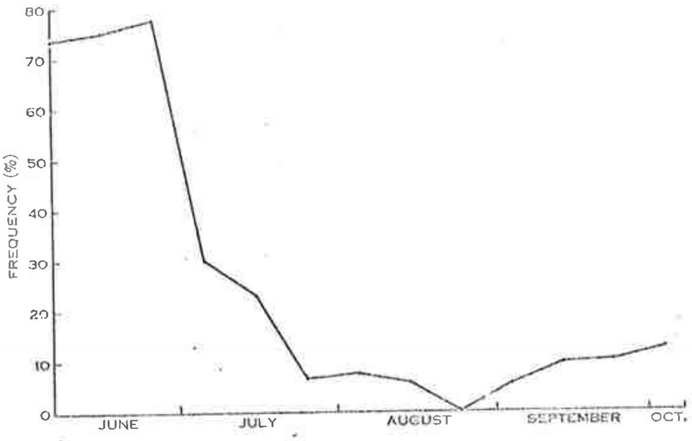

Fig. 3.—Females with milk but no evidence of recent parturition: percentage frequency amongst sexually mature females examined on the Western Australian coast from 1951 to 1955.

To sum up, most of the mature non-pregnant females killed on the west coast of Australia during June have enlarged mammary glands containing milk. The alveoli of these glands are lined with actively secreting cells, indicating that these females are suckling calves. The ovaries and uteri indicate that the previous birth had occurred some months ago. The gunners of the whaling vessels on this coast report that during June many females are accompanied by "yearling" calves. The stomachs of two such "yearlings" (one female 29 ft 3 in. in length shot on June 12, the other, also female, 28 ft 9 in. in length, shot on June 14) were found to contain partly digested milk, proving that these were still suckling.

The above evidence indicates that most young are suckled until the end of June. From Table 2 and Figure 3 it is inferred that most young are weaned towards the end of June or the beginning of July.

TABLE 3

COMPOSITION OF MILK AND MILK RESIDUES FROM 15 FEMALE HUMPBACK WHALES FROM THE WEST COAST OF AUSTRALIA

Stage of Lactation		Date Whale Killed	Composition of Milk					
			Specific Gravity	Total Solids (%)	Fat (%)	Protein (N × 6·38)	Ash (%)	Carbohydrate* (%)
Suckling new-born calf (approx. 1 week after parturition)		3.viii	1·042	35·6	20·4	12·4	1·6	1·2
Just prior to weaning: mammary glands actively secreting		13.vi	1·030	47·1	29·1	—	1·94	—
		14.vi	1·004	54·7	39·2	13·1	1·56	0·8
		15.vi	1·016	46·8	32·6	12·5	1·53	0·2
		15.vi	1·030	41·8	32·4	—	1·80	—
		16.vi	1·015	54·0	37·0	13·6	1·66	1·7
		17.vi	0·992	54·8	41·3	10·7	1·41	1·4
		18.vi	1·008	47·5	26·6	—	1·39	—
		19.vi	0·958	40·5	25·5	11·8	1·55	1·6
	Mean:		1·007	48·4	33·0	12·5	1·61	1·1
Calves just weaned: alveoli involuting and no longer secretory	Left†	15.vii	0·989	63·6	32·0	—	1·01	—
	Right†	15.vii	0·989	63·8	33·6	—	1·01	—
	Left†	18.vii	1·017	42·9	28·5	—	2·04	—
	Right†	18.vii	1·017	42·1	26·8	—	2·09	—
		18.vii	1·018	47·8	31·8	—	1·49	—
	‡	10.viii	—	58·5	54·3	3·0	0·5	0·7
Recently lactating: mammary glands involuting. Residual fluid in mammary ducts after weaning—oestrus cycles recommenced		2.viii	—	6·1	0·4	4·6	1·0	0·1
	Left	9.viii	—	7·6	0·7	4·7	0·9	1·3
	Right	9.viii	—	18·8	12·9	4·3	0·9	0·7

*By difference.

†Milk thicker than usual.

‡Milk extremely thick.

With lactation generally commencing in mid August and weaning taking place at the end of the following June, the average length of the lactation period in the humpback whale is thus $10\frac{1}{2}$ months.

Contrary to the suggestion by Matthews (1937) no evidence has been found of a sudden increase in the length of baleen plates in young whales at the time of weaning.

(c) *Composition of Milk*

Table 3 shows the results from the analysis of milk and milk residues from 15 female humpback whales in progressive stages during and after lactation. In most cases the analysis was performed on a pooled sample from both mammary glands, but on three occasions samples from left and right glands were collected and analysed separately.

In comparison with later stages, the milk from the female shot at the commencement of suckling was already high in protein content (12·4 per cent.). The fat content was also relatively high (20·4 per cent.) but not as high as that in the milk of females during more advanced lactation.

For a short time after weaning, when the mammary glands are enlarged but no longer secretory, some milk of almost normal appearance and composition is found in the mammary ducts (Table 3). At a later stage after lactation when the involution of the mammary glands is more marked there may be some liquid in the mammary ducts, but this usually has the appearance of whitish or turbid yellowish water. The composition of such fluid from two females in this phase is shown at the bottom of Table 3.

V. OVARIAN CYCLES

(a) *Ovarian Activity During Pregnancy*

Unlike the horse (Amoroso, Hancock, and Rowlands 1948) and the African elephant (Perry 1953) where secondary corpora lutea are developed and become functional during pregnancy, the one corpus luteum persists throughout pregnancy in the humpback whale. Proof of this was obtained from several young female humpbacks killed towards the end of the first pregnancy, when the ovaries carried but one corpus graviditatis but no corpora albicantia or luteinized follicles.

The records and ovaries examined by the author at the National Institute of Oceanography in England, and the State Institute for Whaling Research in Norway, showed that the Graafian follicles of pregnant humpback whales taken in Antarctic waters (approximately mid pregnancy) are generally of comparable size (diameters from 10 to 30 mm) to those in non-pregnant anoestrous females.

However, when such females return to temperate waters during advanced pregnancy the majority of the previously well-developed Graafian follicles (those over 10 mm in diameter) have atrophied (Chittleborough 1954). The remaining small follicles (generally up to 6 mm but occasionally reaching 10 mm in diameter) are quite normal, having a large antrum lined by granulosa cells and a cumulus enveloping a normal ovum (Plate 5, Fig. 1). Atretic follicles are very abundant in the ovaries during advanced pregnancy. The ovum within one such atretic follicle had fragmented (Plate 5, Fig. 2). Similar apparent cleavages of ova in atretic follicles have been recorded in other mammals (Boyd and Hamilton 1952, p. 41; Ishida 1953).

In one pregnant female carrying a foetus 12 ft 9 in. in length, Graafian follicles had developed considerably and one follicle 48 mm in diameter was mature. The corpus luteum of pregnancy was in early stages of resorption, similar in size and structure to the condition normally found during early lactation. This case of the initiation of a further ovarian cycle (with resorption of the corpus graviditatis) shortly before parturition must be considered rare in the humpback whale, since in the ovaries of over 70 other females examined during advanced pregnancy there was no development of follicles and no such marked resorption of the corpus graviditatis.

(*b*) *Ovulation Following Parturition Without Loss of Calf*

A lactating female and its young calf were taken on September 15, 1953. The calf, 20 ft 4 in. in length, was considered to be from 2 to 3 months old. The stomach was filled with curdled milk and the intestines contained much bright yellow liquid, so that this calf had been actively suckling.

The maternal mammary glands were actively secreting (Plate 3, Fig. 1) and normal milk was present in the ducts. The recently functional corpus luteum in this female was in early stages of resorption but was still relatively large (95 by 79 by 77 mm), weighing 308 g, and hanging away from the ovary (Plate 2, Fig. 1). In contrast to the general condition during advanced pregnancy, the Graafian follicles of this female in early lactation were well developed, several reaching 22 mm in diameter while one at 34 mm appeared to be maturing. Ovulation had recently occurred, as shown by a developing corpus luteum (59 by 55 by 55 mm), the blood-stained hole at the point of rupture being almost closed by expanding luteal tissue. Thus this female had ovulated soon after parturition.

Another female, killed on August 10, appeared to have recently given birth, as evidenced by a recently functional corpus luteum (104 by 91 by 86 mm, weight 553 g) hanging from one ovary (Plate 2, Fig. 2). The uterine wall was thickened and fibrous, similar to the uterus of the female described above and known to be in early lactation. The mammary glands contained abundant milk and the alveoli were actively secreting. Although the gunner of the catching vessel did not record that a calf was present, the condition of this female strongly indicates that a very young calf was present and being suckled. This female had not ovulated since parturition, but the Graafian follicles were well developed (up to 21 mm in diameter).

Three females taken on the west coast of Australia provided clear examples of post-partum ovulation resulting in pregnancy. When killed (on June 14, 18, and 21 respectively), these females were in advanced pregnancy (foetal lengths 9 ft 3 in., 10 ft 9 in., and 13 ft 0 in.) and yet were in late stages of lactation. In these cases ovulation soon after parturition had resulted in a further pregnancy, so that when killed approximately 10 months after the previous birth they were in advanced pregnancy and also in the last stages of suckling their previous calves.

Further evidence of post-partum ovulation resulting in pregnancy has been obtained from unpublished Norwegian records which the author was permitted to study. Norwegian observers have carefully examined 94 sexually mature female humpback whales taken in Antarctic waters between 1949 and 1955. These females are listed in Table 4 according to the stage in the breeding cycle.

It must be stressed that the percentages given in Table 4 do not represent a random sample of the sexually mature females, as there had been selection, not only by the gunners but also to some extent by the observers, who tended to pay more attention to any lactating females which were taken rather infrequently. With the above reservation, Table 4 shows two important aspects concerning the breeding cycle of female humpback whales.

TABLE 4

SEXUALLY MATURE FEMALE HUMPBACK WHALES (TAKEN IN THE ANTARCTIC FROM 1950 TO 1955) CLASSIFIED BY NORWEGIAN OBSERVERS INTO THEIR RESPECTIVE PHASE OF THE BREEDING CYCLE

Condition	Number	Percentage
Neither pregnant nor lactating (resting)	8	8·5
Pregnant but not lactating	67	71·3
Pregnant and lactating	8	8·5
Lactating but not pregnant	11	11·7
Total	94	

Firstly, of those sexually mature females permitted to be taken in the Antarctic (either pregnant or "resting"), relatively few are "resting" (neither pregnant nor lactating). These few represent those females which had failed to conceive during the previous ovulatory season. Secondly. of the carefully examined lactating females a surprisingly high proportion were concurrently pregnant, which suggests that post-partum ovulation with successful conception is not uncommon in the humpback whale.

Although at present the number of observations upon such females is too small to allow a detailed comparison to be made, it appears that the foetuses carried by lactating females tend to be slightly smaller than foetuses from non-lactating females killed at the same time. This suggests that pregnancies resulting from post-partum ovulation began a little later (perhaps by a month) than most of the pregnancies which began after the previous lactation period.

(c) *Ovulation Following Parturition, After Loss of Calf*

Six females, killed during August and September, appeared from the state of the ovaries and uteri to have recently given birth. The mammary glands were enlarged and milk was present, although in some cases the milk appeared to be more dilute than usual. Histologically the mammary glands of all six were involuting, the alveoli being shrunken, connective tissue increasing, and the gland cells being no longer secretory (see Plate 4, Fig. 2).

This evidence of recent parturition, together with the involution of the mammary glands, strongly suggests that in these cases the calf had been lost at, or very soon after, birth. Yet in five of these six females further oestrous cycles had commenced; in three cases a mature follicle was present, in another ovulation had just occurred, and in the fifth a developing corpus luteum showed that ovulation had recently occurred.

(*d*) *Post-lactational Ovulation*

As shown in Section IV(*b*), lactation in this species continues for approximately 10½ months, most females weaning the calf at the end of June. It has also been shown (Chittleborough 1954) that the majority of mature non-pregnant females experience oestrous cycles during July, August, and September, maturing follicles (pro-oestrus) being most common in July. From this it follows that females do not normally experience a period of anoestrus after lactation. In some cases, as mentioned in Section IV(*b*), oestrous cycles commence during June or early July shortly before lactation has ceased.

VI. DISCUSSION

From the evidence of ovarian activity, near-term foetuses, and new-born calves, the gestation period in the humpback whale occupies nearly 12 months, conception and parturition occurring between June and October, but with maximum frequency of both early in August. Similar results were reported by Matthews (1937), from an analysis of foetal lengths. Conception rarely occurs in the Antarctic; of 250 foetuses taken on the west coast of Australia, only one (4 ft 9 in. long when examined on July 9) could have been conceived in the Antarctic.

The foetal sex ratio is slightly inclined towards males, both for near-term foetuses (51·4 per cent. males) and in earlier stages of pregnancy from the Antarctic (51·9 per cent. males). Higher proportions of male foetuses have been reported from previous Antarctic catches by Mackintosh (1942) (57·4 per cent. males) and Omura (1953) (53·4 per cent. males). As these ratios were based mainly upon smaller foetuses, it might be suggested that a marked excess of males at conception progressively declines during pregnancy so that at birth the sex ratio is only slightly inclined towards males. However, some of the smaller foetuses may have been wrongly sexed. In some of the smaller foetuses the clitoris protrudes quite markedly from the genital groove, and from a brief superficial check can be mistaken for the tip of a penis.

In the humpback whale, ovulation and implantation occur with equal frequency on the left and right sides of the body, unlike the condition in the Odontoceti, where ovulation and pregnancy occur predominantly on the left side (Slijper 1949).

The humpback calf is suckled for approximately 10½ months, lactation being terminated at the end of June in the majority of females. There is no evidence of a sudden increase in baleen growth at the time of weaning (proposed by Matthews

(1937)). As stressed by van Lennep and van Utrecht (1953), weaning is probably a gradual process, the calf suckling less and less frequently as it becomes more independent of the female. Since the calf is not completely weaned until the winter northward migration has taken it away from the Antarctic feeding area, there is no sharp change from a milk to a crustacean diet. A non-feeding period in warmer water (with further growth of baleen) intervenes between weaning and the first season of plankton feeding in the Antarctic.

The composition of the milk is similar to that reported by Clowes (1929), White (1953), Gregory *et al.* (1955), and Ohta *et al.* (1955), for other species of whales and by Pedersen (1952) for the humpback whale.

Previous authors have claimed that the female humpback whale may ovulate, with successful conception, during lactation, but the lack of reliable evidence led Matthews (1937) to reject this theory. Norman and Fraser (1948) state that: "It is believed by one authority that the humpback females become pregnant every year and that pairing takes place again about a month after parturition". Van Lennep and van Utrecht (1953) note that ovulation during lactation is not uncommon in the humpback whale.

Authentic evidence of post-partum ovulation in humpback whales has been slow in accumulating, mainly because females accompanied by calves are protected by international regulation. Evidence must be gleaned over a number of years from the few lactating females which are taken and examined in detail. Conception from a post-partum ovulation results in a female being pregnant and lactating at the same time. However, some whaling inspectors, under the impression that a whale cannot be simultaneously pregnant and lactating, may record the pregnancy but overlook the concurrent lactation.

There is now an increasing amount of reliable evidence that in the humpback whale post-partum ovulation does occur and may result in a further pregnancy while the female is suckling the previous calf. From the Antarctic, Norwegian observers have carefully examined eight female humpbacks which were simultaneously lactating and pregnant, and van Lennep and van Utrecht (1953) have reported another female humpback in the same condition. The evidence from the west coast of Australia is at present confined to one recently ovulated female and its calf which were killed soon after parturition, and three females in both late lactation and advanced pregnancy when killed in June.

It is possible that if more female humpback whales were examined soon after parturition it would be found that post-partum ovulation (followed by lactation anoestrus) is of regular occurrence in this species. It might be argued that if post-partum ovulation occurs regularly, the present investigation on the west coast of Australia should have revealed more cases (in June) of females in both late lactation and advanced pregnancy. Two factors could explain this. In the first place, conception might less often succeed at post-partum ovulation than from oestrous cycles at the end of lactation (as reported by Brambell and Hall (1936) in the lesser shrew). Secondly, pregnant females reach the Australian coast each winter later than most of the non-pregnant mature females, so that by the time the pregnant females reach this area in July and early August, any calves being suckled during pregnancy would have been weaned. As indicated in Figure 2, very few females in advanced pregnancy are taken on the west coast of Australia during June. Only two pregnant females were examined by the author during June and these were both in late stages of lactation.

Along the west coast of Australia some females lose their calf at or shortly after parturition. Some of these losses may be due to sharks or to killer whales (Chittleborough 1953). It has been shown that in such cases the female recommences oestrous cycles at once. This is similar to the condition in the mouse, where Parkes (1926) found that: "Normal oestrous cycles succeed parturition immediately in the absence of suckling".

If the calf is suckled for the normal period and post-partum ovulation either did not result in pregnancy or did not occur, the female remains in anoestrus until the termination of suckling, at which time (the end of June in most females) oestrous cycles recommence.

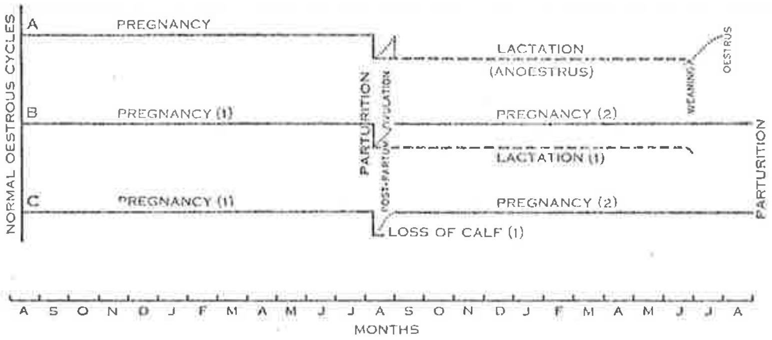

Fig. 4.—Types of breeding cycles found in sexually mature female humpback whales.

Figure 4 summarizes the three types of breeding cycles which have been demonstrated in sexually mature female humpback whales. In the first (Fig. 4*A*), absence of post-partum ovulation, or its occurrence without conception, results in one calf in 2 years. The majority of the breeding cycles in the humpback are of this type. If post-partum ovulation is of regular occurrence, this might help to explain the relatively rapid rate of accumulation of corpora albicantia suggested by some authors (Matthews suggested up to five ovulations in each 2-year breeding cycle).

Figure 4*B* shows a successful post-partum ovulation resulting in two calves in 2 years. Although this type of cycle may commonly occur in female humpback whales it should be noted that this cycle, being slightly longer than that of type A, cannot be maintained continuously by any individual. The post-partum ovulation would occur later (perhaps by a month) each year, progressively lessening the possibility of fertilization. It is probable that after one cycle of type B, a female would revert to a cycle of type A.

In Figure 4*C*, loss of the first calf at or just after parturition is balanced by pregnancy succeeding immediately afterwards. In such cases there would be two pregnancies in 2 years but only one calf reared. This condition is less obvious as it can be diagnosed only within a short period after the first parturition, but it is suggested that it is not uncommon in the humpback whale.

VII. ACKNOWLEDGMENTS

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EXPLANATION OF PLATES 1–5

Plates 1, 3, 4, 5 prepared from sections 7 μ thick, stained with haematoxylin and eosin, using ×45 apochromatic lens, Wratten 11 filter, and microfile film. Magnification in these plates, ×640.

PLATE 1

Fig. 1.—Mammary gland of female in advanced pregnancy. Alveoli well developed, nuclei enlarged and vesicular. No secretion in majority of alveoli, but occasionally a smooth acidophilic secretion (*upper right*).

Fig. 2.—Mammary gland of female in advanced pregnancy. Alveoli well developed, nuclei irregular and darkly staining. Abundant granular basophilic secretion in alveoli.

PLATE 2

Fig. 1.—Ovaries of a female killed shortly after parturition and known to be suckling a calf. Recently functional corpus luteum (95 by 79 by 77 mm, weight 308 g) extending from top of right ovary. Newly formed corpus luteum (59 by 55 by 55 mm) on lower right ovary. Graafian follicles well developed, to 22 mm in diameter, one 34 mm, maturing. (Mammary gland tissue from this female shown in Plate 3, Fig. 1.)

Fig. 2.—Ovaries of a female killed shortly after parturition and considered (but not proven) to be suckling a young calf. Recently functional corpus luteum (104 by 91 by 86 mm, weight 555 g) extending from left ovary. Graafian follicles well developed, to 21 mm in diameter. Histological examination showed that the mammary glands were actively secreting milk.

PLATE 3

Fig. 1.—Actively secreting mammary gland of a female killed shortly after parturition and known to be suckling a young calf.

Fig. 2.—Actively secreting mammary gland of a female in late lactation, killed on June 13. Largest corpus albicans in the ovaries of this female measured 61 by 52 by 48 mm.

PLATE 4

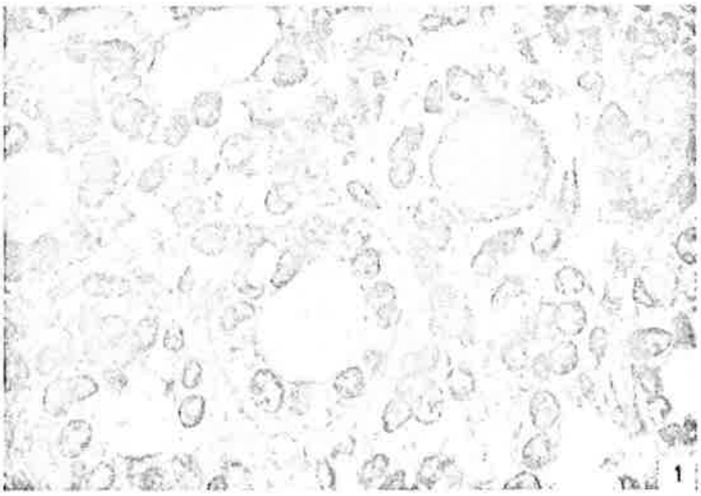
Fig. 1.—Mammary gland of female killed on August 10 soon after weaning the calf in the normal manner. Thick white "milk" (54·5 per cent. fat) present in the ducts, but alveoli regressing and not secretory. Largest corpus albicans measured 49 by 47 mm.

Fig. 2.—Mammary gland of female which had recently given birth but had lost the calf. Rich white milk present in ducts but alveoli resorbing and not secretory. Recently functional corpus luteum (92 by 82 by 77 mm, weight 370 g) hanging from one ovary, and enlarged uteri indicate recent parturition.

PLATE 5

Fig. 1.—Normal ovum (92 μ diameter) within a 5 mm follicle from an ovary of a female in advanced pregnancy.

Fig. 2.—Fragmenting ovum within an atretic follicle from the same ovary as that of Fig. 1. Note zona pellucida still present but absence of granulosa cells.



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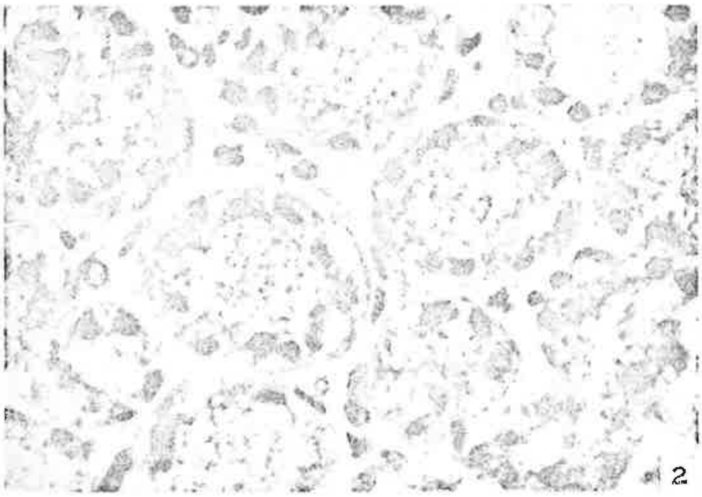

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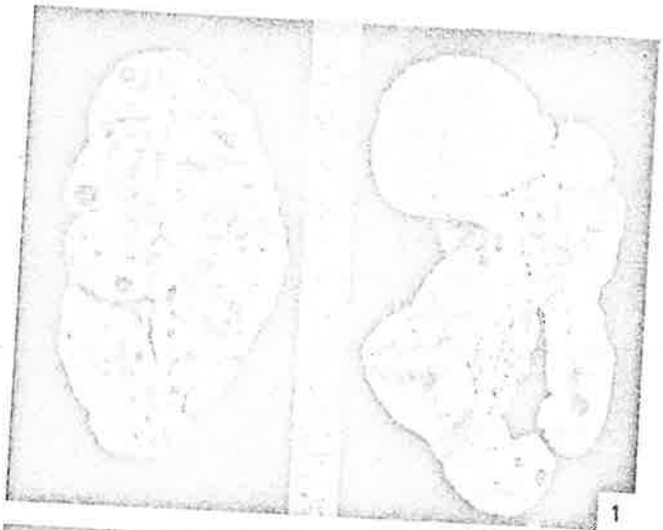
PLATE 2

BREEDING CYCLE OF FEMALE HUMPBACK WHALE



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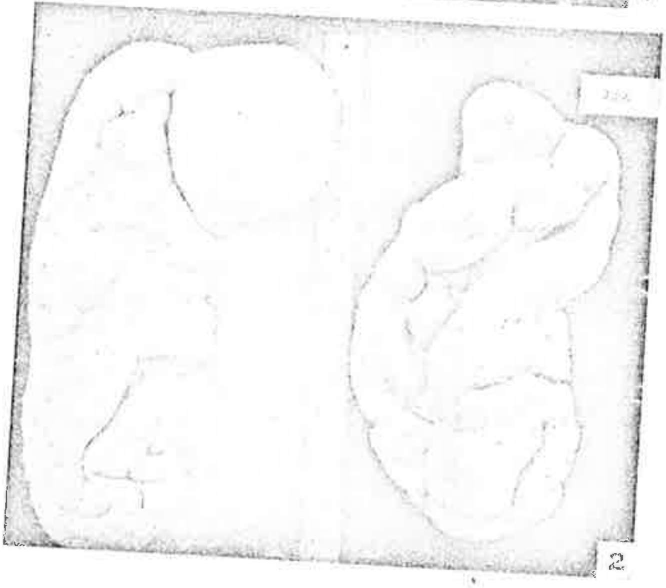

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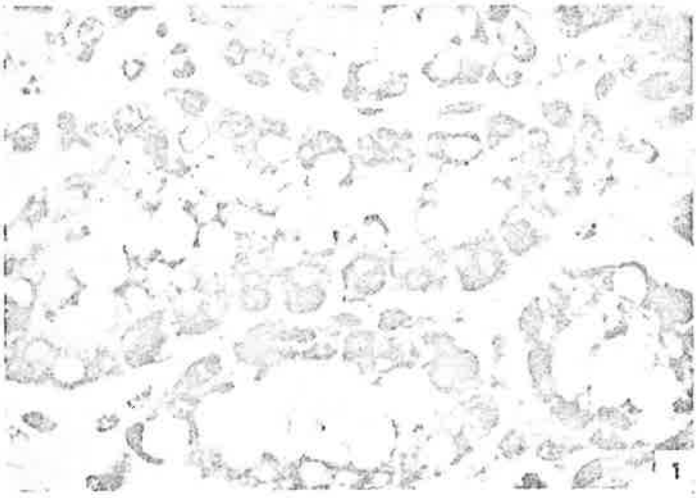

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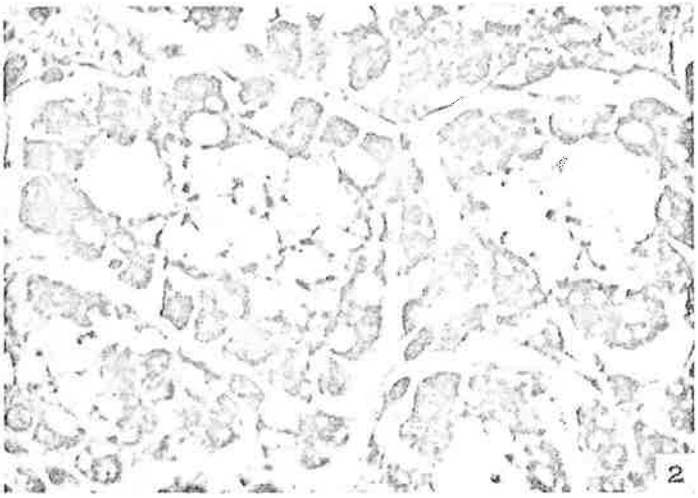

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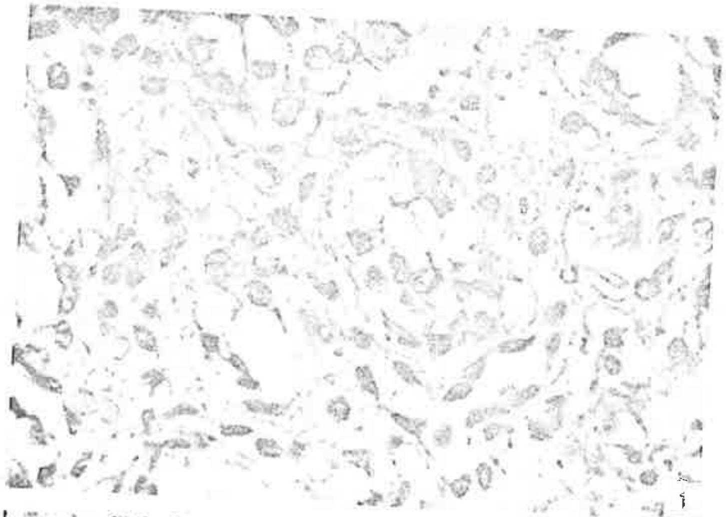

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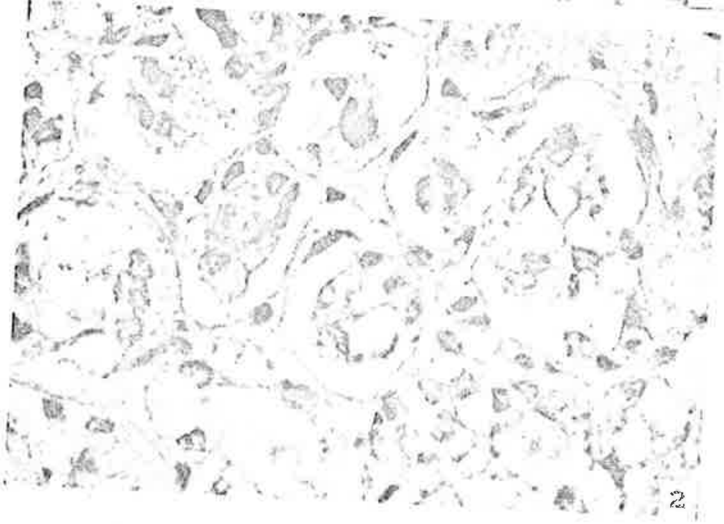

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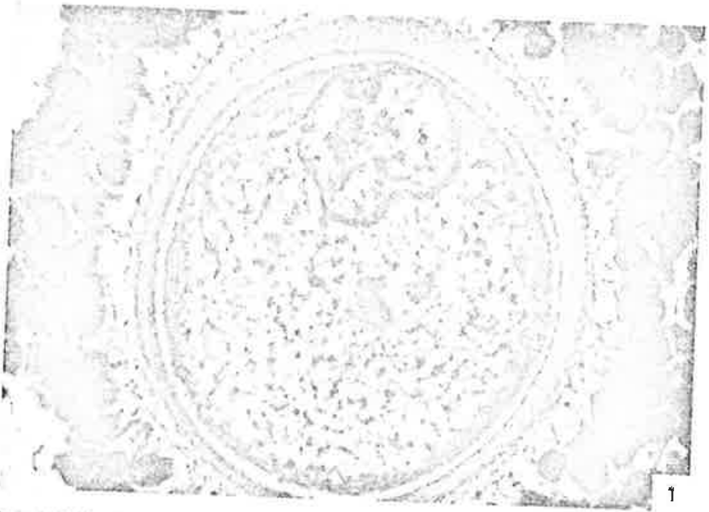
BREEDING CYCLE OF FEMALE HUMPBACK WHALE



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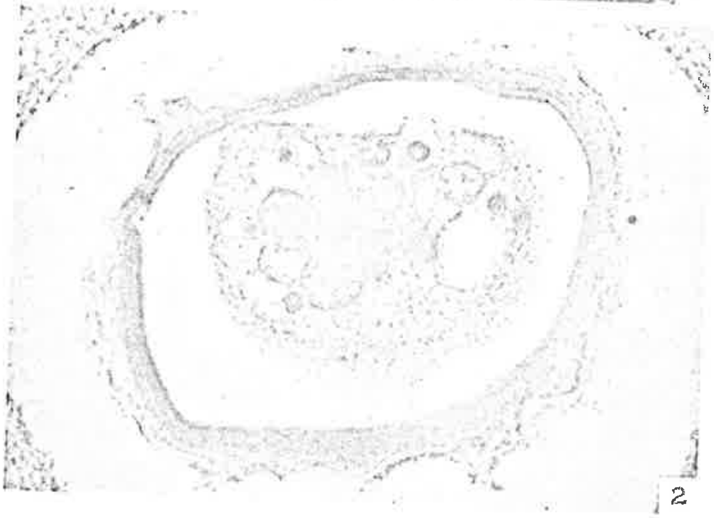

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Paper 5

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AERIAL OBSERVATIONS ON THE HUMPBACK WHALE, *MEGAPTERA NODOSA* (BONNATERRE), WITH NOTES ON OTHER SPECIES

By R. C. CHITTLEBOROUGH

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Australia

AERIAL OBSERVATIONS ON THE HUMPBACK WHALE, *MEGAPTERA NODOSA* (BONNATERRE), WITH NOTES ON OTHER SPECIES

By R. G. CHITTLEBOROUGH*

(*Manuscript received May 27, 1953*)

Summary

Aerial observations of humpback whales in the region of Point Cloates, Western Australia, during 1952 are recorded. The first southward-moving humpback whale was sighted on July 21, while decreasing numbers were seen moving northwards until early October. In 1952 the change from a predominantly northward migration of humpback whales to a southward migration occurred close to August 24. The speed of migration of a number of these whales is recorded, the mean value being 4.3 kt. A few humpback whale calves were sighted early in July and a peak in their occurrence in August suggests maximum frequency of parturition early in August. A very great increase in the occurrence of calves in the area late in the season suggests that female humpback whales rearing calves move southwards later than other individuals. Some evidence is presented that Exmouth Gulf is a nursery area.

The presence of some killer, fin, blue, and minke whales in the area is noted.

I. INTRODUCTION

The Norwest Whaling Company, operating from a shore station at Point Cloates on the Western Australian coast, engages a pilot flying an Auster aircraft for the purpose of locating suitable humpback whales to be taken by the catching vessels.

Under normal conditions at an altitude of 800-1000 ft it is possible to distinguish not only the species of whale and whether a calf is present but also, after some experience, whether a humpback whale is large enough to be taken by the catching vessels.

From July to early October 1952, by the ready cooperation of Mr. J. F. Pekin, the pilot of the aircraft, numerous aerial observations were made on whales and their movements in the region of Point Cloates. The author accompanied the pilot on a number of the flights.

The observations obtained are recorded and discussed in the present report. Most of the records are on the humpback whale (*Megaptera nodosa* Bonnaterre) and concern the direction and speed of migration, the presence of new-born calves, and the possibility that Exmouth Gulf is a "nursery" area for the species.

The aerial photographs of humpback whales used in this report were taken some years ago off the West Australian coast by an officer of this Division, Mr. S. Fowler, while engaged upon fisheries exploration flights.

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* Division of Fisheries, C.S.I.R.O., Cronulla, N.S.W.

From a large number of photographs then obtained, these have been selected as showing typically the appearances upon which the facts presented in this paper are based. The photographs were taken at lower altitudes than those maintained during the flights when the present observations were made.

II. Humpback Whales

(a) *Direction of Migration*

In order to find the time when the migration of the humpback whales in the area changed from a northward to a southward movement, a record was made as often as possible of the direction of movement of whales sighted from the aircraft. This was noted for 560 humpbacks in the neighbourhood of Point Cloates between June and October 1952. In almost every case the direction was within a few degrees of north or south.

Table 1

Humpback Whales off Point Cloates: Direction of Migration

Seven-Day Period Ending	Moving North		Moving South	
	Number	Percentage	Number	Percentage
8.viii.52	12	92.3	1	7.7
15.viii.52	21	75.0	7	25.0
22.viii.52	58	81.7	13	18.3
29.viii.52	61	43.0	81	57.0
5.ix.52	11	21.2	41	78.8
12.ix.52	15	22.7	51	77.3
19.ix.52	8	10.7	67	89.3
26.ix.52	3	7.9	35	92.1
3.x.52	1	2.6	38	97.4
10.x.52	1	2.7	36	97.3

In June and July almost every humpback whale observed from the air was moving northwards. Towards the end of July the first southward-moving humpbacks were sighted, the first one on July 21, and two more on July 30. From the beginning of August southward-moving humpbacks were seen with increasing frequency.

In Table 1 the proportions moving north and south are shown for weekly periods from August to early October. The weekly totals do not indicate the total number of humpback whales sighted, as whales were often seen to blow too far distant to observe the direction they were travelling, and these could not always be examined as nearer whales were under observation at the time. However, the series shown in Table 1 may be regarded as a random sample.

From Table 1 the curves in Figure 1 have been drawn to indicate the trends in humpback whale movements off Point Cloates in 1952. This figure shows that the change from a predominantly northward migration to a southward one occurred close to August 24, but that this change was not abrupt. There were still occasional humpback whales moving northwards early in October. One whale observed from the air moving northwards near Point Cloates on October 1, 1951, was a large, very rotund individual travelling alone and was considered by the pilot to be a female in late pregnancy.

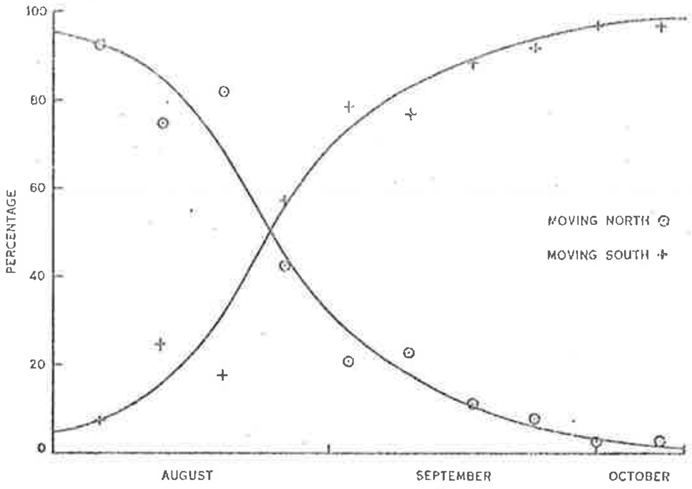

Fig. 1.—Humpback whales off Point Cloates, 1952. Proportions moving north and south.

In his account of earlier operations at Point Cloates Dakin (1934) refers to the time of onset of the southerly migration. He observes (p. 176) that off Point Cloates in 1912 the humpback whales began returning south about August 24, while in 1913 (p. 195) the southward movement began early in August, reaching its peak by August 17.

Although the time of change from northward to southward migration might vary a little from year to year, the observations made in 1952 show that this change is spread over 10 wk and that in 1952 equal numbers were moving northward and southward close to August 24 (Fig. 1).

(*b*) *Humpback Whale Speeds*

As far as can be ascertained, no records have previously been published of the speeds at which humpback whales swim in the undisturbed state. It is generally accepted that they travel at a slower rate than other species such as fin and blue whales. Gunther (1949) states that fin whales (*Balaenoptera physalus* Linné) at times keep abreast of a ship travelling at 10-12 kt and occasionally travel for short distances at an estimated 16-18 kt. However, these whales were not on an undisturbed migration.

In the region of Point Cloates it was possible at times to fix the position of a selected humpback whale or group observed from the air and to check the position of the same whale or group some hours later. From such records the speeds of migration of these humpback whales were calculated, with the results shown in Table 2.

The records are separated into two series, those where a calf was present and those without calves. Generally a whale with a calf travelled more slowly than whales without a calf. In two cases the calf had only recently been born, as indicated by its very light colour and small size (Plate 1, Fig. 1). In both cases the cow and young calf were travelling slowly, at average speeds of 2.8 and 3.5 kt respectively. It has been found by the author that near-term foetuses always have very lightly pigmented skin, this character persisting for a short time after birth. As the calf grows it darkens as shown in Plate 1, Figure 2. Such cow and calf pairs then travel slightly faster. The average speed of the humpback whales in Table 2 was 4.3 kt.

TABLE 2

HUMPBACK WHALE SPEEDS, POINT CLOATES

Date Observed	Type of Group	Times Observed		Total Hours	Nautical Miles Travelled	Direction	Speed (kt)
		From	To				
15.viii.52	3 Cow-calf pairs*	0800	1230	4.5	11.5	N	2.6
10.ix.52	Cow-very young calf	1030	1140	1.17	3.3	N	2.8
6.x.51	Cow-calf	1350	—	—	—	—	3.0
6.x.51	2 Adults-1 calf	1345	1615	2.5	7.5	—	3.0
29.viii.52	2 Adults-1 calf	0735	1015	2.67	8	N	3.0
18.viii.52	Cow-calf	0815	1100	2.75	9	N	3.3
21.vii.52	Cow-very young calf	0930	1100	1.5	5	N	3.3
		1100	1515	4.25	15.25	N	3.6
		0930	1515	5.75	20.25	N	3.5
28.viii.52	Cow-calf	0730	1030	3	11	N	3.7
27.vii.52	Cow-calf	0855	1210	3.25	12.5	N	3.85
14.vii.52	Cow-calf	0955	1210	2.25	9	N	4.0
		1210	1520	3.17	12	N	3.8
		0955	1520	5.42	21	N	3.9
11.x.51	Cow-calf	0800	1515	7.25	32	S	4.4
1.ix.52	Cow-calf	1000	1040	0.67	3	N	4.5
15.vii.52	Cow-calf	1550	1700	1.17	6	N	5.15
7.viii.52	Cow-calf	1020	1210	1.83	11.8	N	6.4
6.viii.52	Cow-calf	0800	1130	3.5	27	N	7.7
3.viii.52	2 Adults	1130	1555	4.42	16	N	3.6
30.vii.52	2 Adults	0930	1015	0.75	3.2	N	4.26
16.vii.52	3 Adults	0950	1430	4.67	20	N	4.3
15.vii.52	1 Adult (large)	0845	1045	2.0	10.75	N	5.4
11.vii.52	1 Adult	1215	1535	3.33	19	N	5.7
17.vii.52	1 Adult	0915	1020	1.08	7	N	6.5

* Three pairs from ½ to 1½ miles apart; maintained their relative positions over 4½ hr.

(c) *Presence of Calves amongst Humpback Whales off Point Cloates*

A record was kept of humpback calves sighted from the aircraft. Usually a calf accompanied a single adult, but sometimes two adults were present. The dates on which the first calves were seen and when the proportion of calves in the sightings first rose considerably should give further evidence on the time of parturition. To this end, the total numbers of calves observed in weekly periods were expressed as percentages of the weekly total numbers of adult humpbacks observed sufficiently closely to establish whether or not a calf was present. These weekly totals and percentages are shown in Table 3 and the percentages graphed in Figure 2.

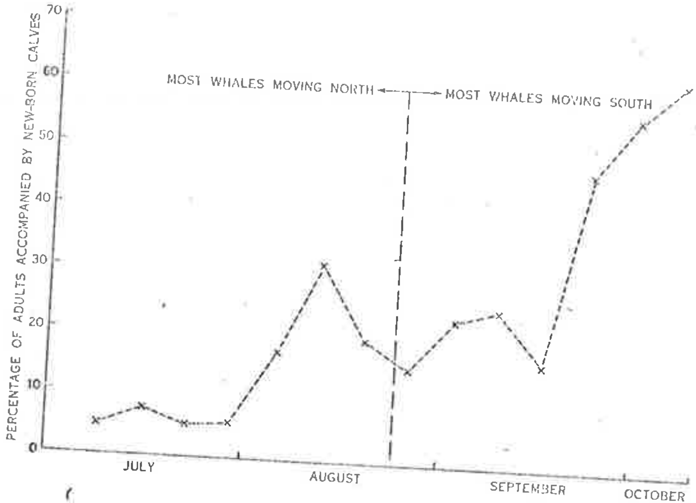

Fig. 2.—Occurrence of humpback whales off Point Cloates, 1952.

A small proportion of calves was present early in July at the commencement of the aerial observations. From this it would seem that parturition in a few cases must have taken place late in June or even earlier.

In August calves were of relatively common occurrence, as shown in Figure 2, the peak in the second week suggesting a high frequency of births early in August. This confirms Matthews's (1937) conclusion, based on a consideration of foetal lengths, that in the humpback whale maximum frequency of parturition occurred in August.

In late August and the first half of September, when the majority of humpback whales were moving south (Fig. 1), the proportion of calves remained relatively constant; but in late September and early October the proportion of calves amongst the humpback whales observed off Point Cloates greatly increased (Fig. 2). Almost all the calves then seen were much darker and slightly larger than those seen shortly after birth. The very high rise in the proportion of these calves late in the season suggests that the majority of cows rearing calves begin their southward migration later than other individuals.

(d) *Humpback Whales in Exmouth Gulf*

Exmouth Gulf is a large, relatively shallow gulf a few miles north of Point Cloates. While whale-spotting during the 1951 catching season, Mr. J. Pekin noted that in September there were large numbers of adult humpback whales with calves in this gulf, indicating that it was a nursery area for this species. It was hoped that in 1952 aerial surveys could be made of this gulf at intervals through the winter and spring, but no such flights could be made until late September. The results of three surveys are summarized in Table 4.

Table 3

PROPORTIONS OF CALVES AMONGST THE MORE CLOSELY OBSERVED HUMPBACK WHALES OFF POINT CLOATES

Seven-Day Period Ending	Total Adults Checked for Calves	Calves Sighted	
		Number	Percentage
11.vii.52	41	2	4.9
18.vii.52	122	9	7.4
25.vii.52	100	5	5.0
1.viii.52	69	4	5.8
8.viii.52	75	13	17.3
15.viii.52	64	20	31.3
22.viii.52	72	14	19.4
29.viii.52	79	12	15.2
5.ix.52	52	12	23.1
12.ix.52	56	14	25.0
19.ix.52	48	8	16.7
26.ix.52	40	19	47.5
3.x.52	39	22	56.4
10.x.52	37	23	62.2

Table 4

AERIAL SURVEYS OF HUMPBACK WHALES IN EXMOUTH GULF, 1952

Date	Humpback Whales Sighted				Percentage of Adults with Calves
	Single Adults	Cow-calf Pairs	Adult Pairs	Groups of 3 Adults	
24.ix.52	—	17	6	1	53
30.ix.52	—	8	—	—	100
9.x.52	—	17	3	—	74

While Table 4 shows that a high proportion of the humpback whales in this gulf were accompanied by calves, these surveys were made too late in the season to show that large numbers of females gather here when rearing calves.

III. Other Species of Whales in the Region of Point Cloates

(*a*) *Killer Whales* (Orcinus orca *Linné*)

Schools of this species were sighted on a number of occasions off Point Cloates during 1952. The records are summarized in Table 5.

Table 5

KILLER WHALES SIGHTED OFF POINT CLOATES IN 1952

Date	Number	Direction	Remarks
17.viii.52	5	S	—
24.viii.52	*c.* 50-60	S	Amongst a stream of southward-moving humpbacks which appeared to be changing direction more than usual
	Several	N	Close to six humpbacks moving south
9.ix.52	*c.* 40	S	Close to three adult humpbacks moving south
11.ix.52	Over 30	—	Appeared to be coming in from west, closing in on several humpbacks

In addition to these, large numbers of killer whales, estimated by Mr. J. Pekin as at least 150, were seen in Exmouth Gulf during a survey flight on September 24. Apart from hunting by man, the mortality rate amongst humpback whales is probably highest immediately after birth and at this stage killer whales may make successful attacks. In October 1951, Mr. J. Pekin observed in Exmouth Gulf four or five killer whales attacking a group of humpback whales consisting of two adults and a calf. One adult humpback (presumably the cow) kept the calf very close, while the other adult (possibly a bull) charged the killer whales, beating them off with its flukes. A very similar incident occurred off Point Cloates in the 1952

Table 6

FIN AND BLUE WHALES OBSERVED OFF POINT CLOATES, 1952

Date	Species	Number	Distance Off Shore (miles)	Direction	Remarks
12.ix.52	Blue	1	5	S	—
17.ix.52	Blue or fin?	1	8-9	S	—
1.x.52	Fin	1	3	S	Length approx. 70 ft.
3.x.52	Fin	2	10	S	Cow and calf
4.x.52	Fin	1	20	S	—
5.x.52	Fin	2	—	S	—
	Fin	2	—	S	—
	Fin	1	—	S	—
	Fin	1	—	S	—
	Fin	1	—	S	—
	Blue	2	—	S	—
6.x.52	Fin	2	10-11	S	—
10.x.52	Fin	2	6	S	Cow and calf

season. In neither case were the killer whales seen to be successful in their attacks.

(*b*) *Fin Whales* (Balaenoptera physalus *Linné*) *and Blue Whales* (Balaenoptera musculus *Linné*)

These were sighted only in September and October and were all travelling south. Table 6 gives details of those sighted.

(*c*) *Minke Whales* (Balaenoptera acutorostrata *Lacépède*)

On August 25, 1952, three minke whales were closely observed by the author from the aircraft. These whales, approx. 25-30 ft in length, had the characteristic white band across the flippers. They were in shallow water very close to the reef and were moving south. Another minke whale was sighted off Point Cloates on August 30.

IV. ACKNOWLEDGMENTS

The author wishes to express his gratitude to Mr. J. F. Pekin, pilot of the spotting aircraft, for his enthusiastic cooperation in the collection of these records, and also to the Norwest Whaling Company for their cooperation and for the use of facilities at their station.

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AERIAL OBSERVATIONS ON THE HUMPBACK WHALE

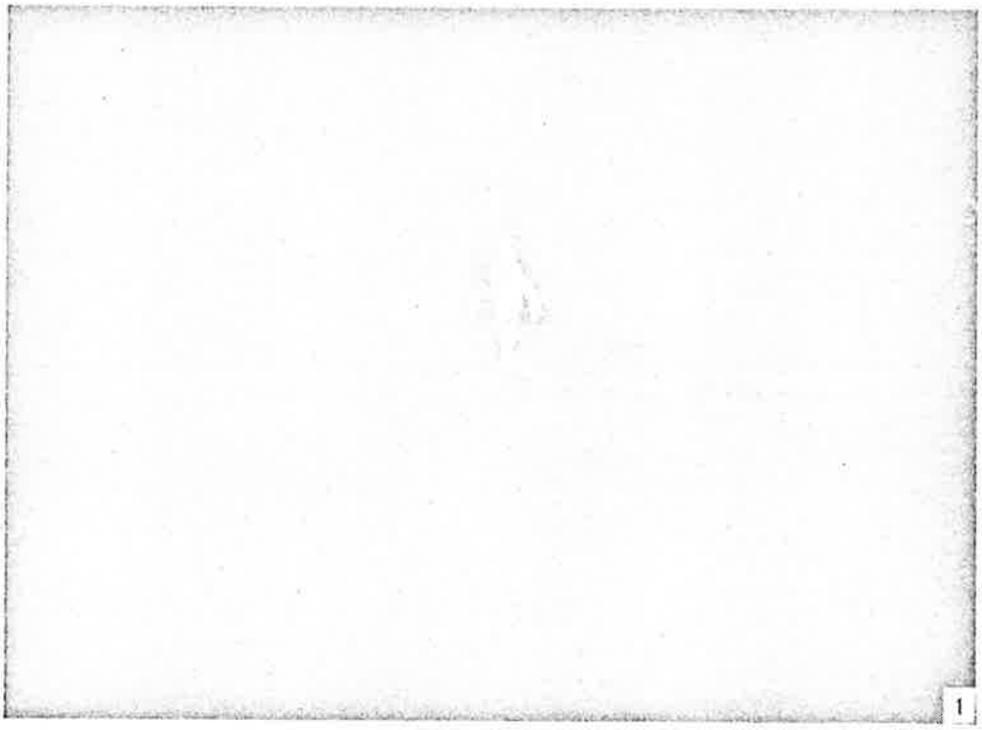
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Fig. 1.—Aerial photograph of female humpback whale with very young calf, Western Australian coast. (Photos: S. Fowler.)

Fig. 2.—Aerial photograph of humpback whale and calf; Shark Bay, Western Australia.

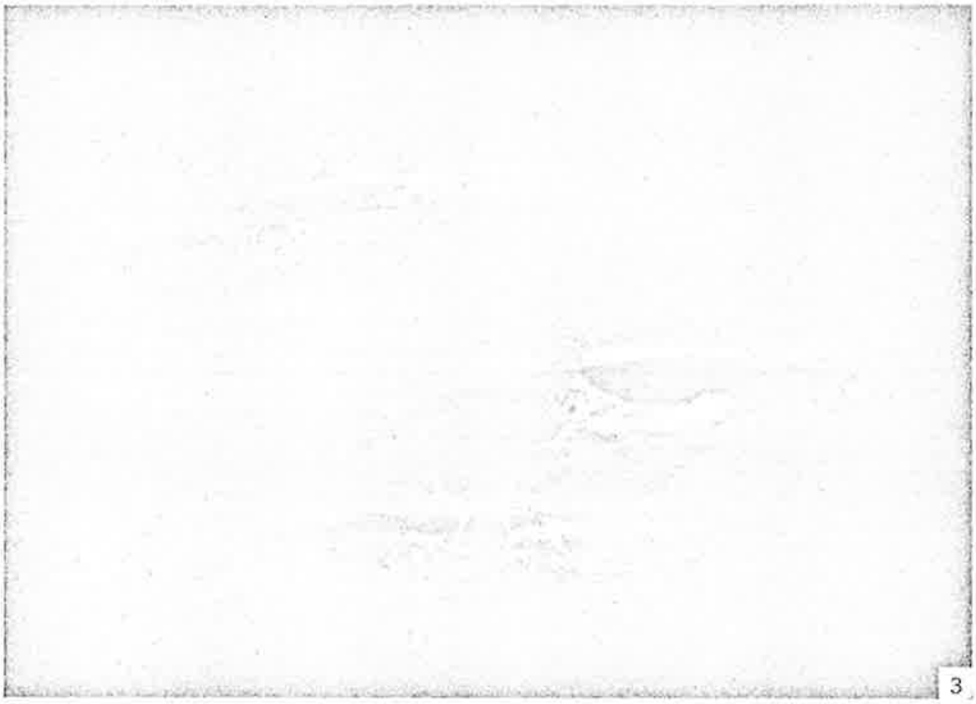

Fig. 3.—Aerial photograph of three humpback whales at the surface, Western Australian coast. (Photos: S. Fowler.)

Fig. 4.—Aerial photograph of two humpback whales sounding, Western Australian coast.

Paper 6

Commonwealth of Australia.
COMMONWEALTH SCIENTIFIC AND
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A Review of Whale Marking and some Trials of a modified Whale Mark

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Introduction.

On the Australian coast, the marking of humpback whales *(Megaptera nodosa)* is carried out as part of the programme of research on this species. The planning of this marking has prompted a reconsideration of the objectives in marking whales. When discussing these aims and the marking techniques widely used at present, it was felt that some improvement is desirable. Discussions with whale research workers in other countries have shown that this opinion is shared by others. It is intended here to review briefly the aims and progress of whale marking, and to describe a modified mark and its behaviour under test.

Aims of whale marking.

Ideally, the aims of whale marking are to obtain direct information on the following aspects:—

(I) Migration and dispersal. These are the simplest objectives since whales of any age may be used and even a low percentage of marks recovered will yield very useful information. Marking has already added considerably to our knowledge of whale movements (Rayner, 1948; Brown, 1954, 1956), but more detailed information is being sought in certain cases, for example the dispersal of humpback whales in South Pacific waters (Dawbin, 1956).

(II) Age and growth rate. If whales of known age can be marked, recoveries in later years will enable us to obtain more precise information upon the growth rate of whales and the age at which breeding commences. Knowing the age of these marked whales when killed, it will be possible to check upon the various indirect methods of age determination which are now in use.

(III) Rate of breeding. Our present evidence upon this is rather circumstantial. Later examination of females which had been marked when they were in a recognizable phase of the breeding cycle, will give very desirable evidence of the breeding rate of individual whales.

(IV) Population size. If the limits of, and the movements within, a particular whale population are known and if an efficient whale mark is used on a sufficiently large scale, it is possible to plan a marking programme which will allow the percentage of recoveries to be used in obtaining a reliable estimate of the size of that population.

A review of previous marking.

The mark at present used in whale research consists of a numbered, stainless steel tube, 23 cms. long, with a lead point anteriorly. Fired from a strongly built shot gun, the mark is intended to lodge in the dorsal muscles of the whale. This method was developed by «Discovery Investigations» in 1926, and up to 1939 about 5,350 whales have been marked in this way (Rayner, 1940, 1948). A total of little over 300 of these marks has so far been recovered. Since the last war, whale marking has been continued on a smaller scale, using the same type of mark, by scientists of at least eight countries.

Provided that it penetrates completely beneath the blubber, this mark can remain permanently in the whale. One mark recovered in 1956 had been carried by a fin whale for 21 years (Brown, 1956). (Marks which lodge only in the blubber, without full penetration, appear to fall out in a relatively short time.) This type of mark has been carefully tested upon dead and living whales (Ruud, Clarke and Jonsgård, 1953, Ruud and Øynes, 1954), showing that with adequate care, the mark rarely lodges in a position likely to be dangerous to the wellbeing of the whale.

However, while this method has yielded valuable information concerning the movements and migrations of the larger species of whales, it has supplied negligible results upon age, growth rate, breeding and population size. Without underrating the value of the results so far obtained, two important deficiencies in this technique must be considered.

Firstly, the mark is suitable only for the larger individuals. Because of the relatively thin blubber in calves, and the size and penetrating power of the mark, there is a considerable danger of causing serious injury or even death to calves. This means that generally only the larger specimens are marked. With these we have no knowledge of the age of individuals when marked. This is a very serious fault in any branding or tagging scheme which aims at anything more than information upon dispersal and migrations. Those who use this type of mark are fully aware of this deficiency. Mackintosh (1952) says, «One of the most urgent needs of all is to mark young whales and breeding whales. If some marks can be recovered (with adequate particulars) after short and longer periods from whales which, at the time of marking, were young calves or were in observed stages of the breeding cycle, a great stimulus could be given to nearly all investigations on the breeding, growth and age of whales.»

Off the Western Australian coast we have attempted to mark whales of known age by marking «yearling» humpbacks which return to this coast during June in company with their mothers. Dawbin (1956), has also marked «yearling» humpbacks in New Zealand waters. However, the identification of yearlings at sea is not infallible, as it was found that even experienced persons sometimes mistake a two year old for a yearling. This was demonstrated in one case when a «yearling» was to be killed for research purposes (under special licence). The specimen obtained proved to be almost two years of age. The most reliable method of marking whales of known age is to mark the calves.

At the meeting in London, 1956, the Scientific Committee of the International Whaling Commission urged that «more attention should be paid to the possible marking of calves».

The second serious drawback in the «Discovery» marks is that being completely embedded in the body, they are frequently missed at the factory. Rayner (loc. cit.) has draw attention to this aspect. On the basis of trials carried out in the Antarctic, Ruud and Øynes (1954) estimated that 50 % of the marks which come aboard factory ships pass through the factory without being discovered. They also found that approximately one third of the recovered marks were not discovered until the residues were removed from the cookers. At this stage it is of course almost impossible to relate the mark to one particular whale, and even if this were occasionally possible it would be too late to obtain the necessary material such as gonads, baleen, ear plugs, etc. from the whale.

If the percentage of whale marks recovered is to be used as a means of calculating the size of the population, the efficiency of recovery needs to be much improved.

With the aim of increasing the efficiency of recovery of marks, Professor Ruud (see Ruud, Clarke and Jonsgård, 1953) adapted the «Discovery» mark by attaching coloured nylon streamers. These did not appear to affect the trajectory of the mark, and tests (upon dead whales) showed that the streamers hung from the side of the whale, considerably increasing the possibility of discovering the mark. The prompt location of marks by external signs allows a detailed examination of the marked whale to be made. However, «streamer» marks recovered since 1953 generally had little or none of the nylon streamers still attached. In Japanese trials with streamer marks, Omura and Kawakami (1956) found that if the streamers were beneath the carcass as it was hauled up the slipway, they were easily torn off.

Even if the streamer mark had a higher rate of recovery than the original mark, there has been no adaption of the mark itself for use on calves.

The important point in marking calves is that recoveries in later years will provide us with material from whales of known ages. From this material it will be possible to clarify much of the present work upon age, growth rate, sexual maturity, breeding etc. Various methods, such as body length, numbers of ovulations, epiphysial fusion in vertebrae, variation in baleen thickness, and most recently, the laminations within ear plugs, have been used, either singly or in various combinations, for age determinations. *But none of these methods have been standardised against whales of known age.* Until this has been done all the present methods of age determination will depend more or less upon the interpretation favoured by individual scientists.

In order to mark the calves of the larger spe-

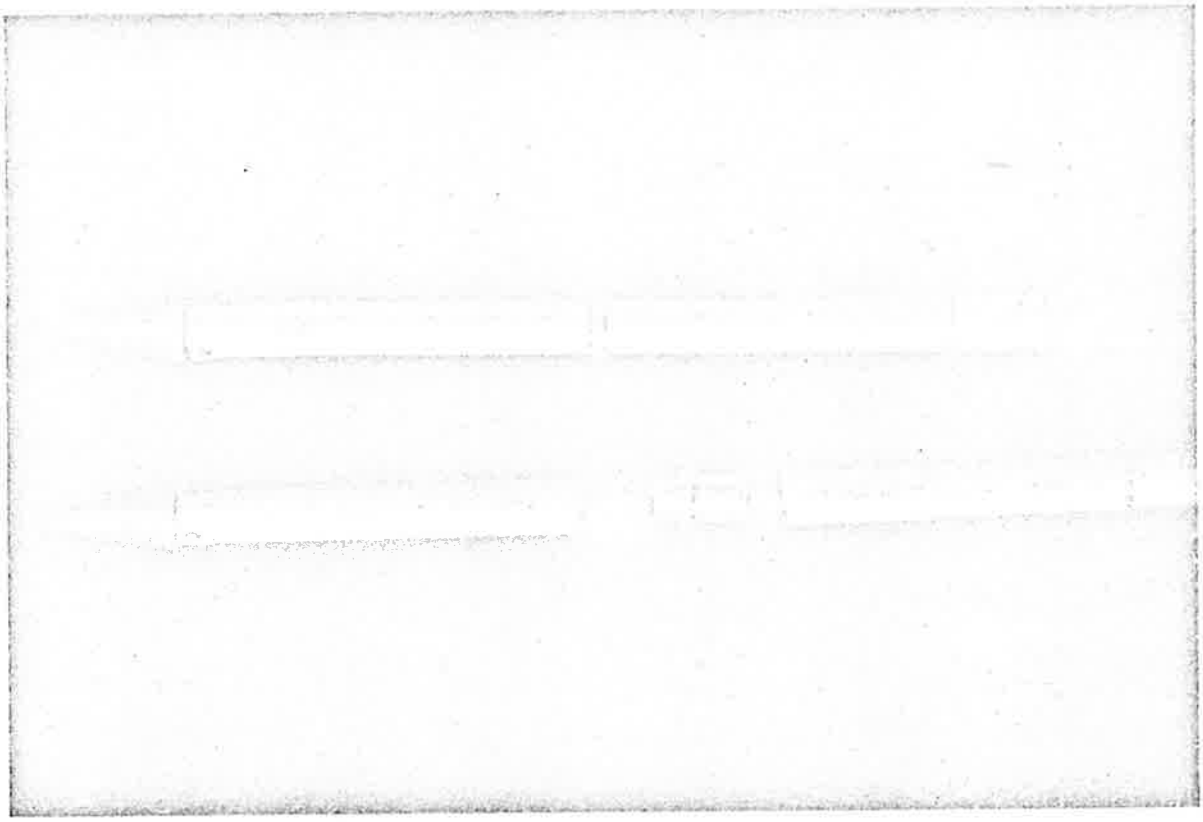

Figure 1. Modified whale marks. Upper mark as fired, lower mark separated to show components. In all later marks, the collar was centrally placed on the stopper.

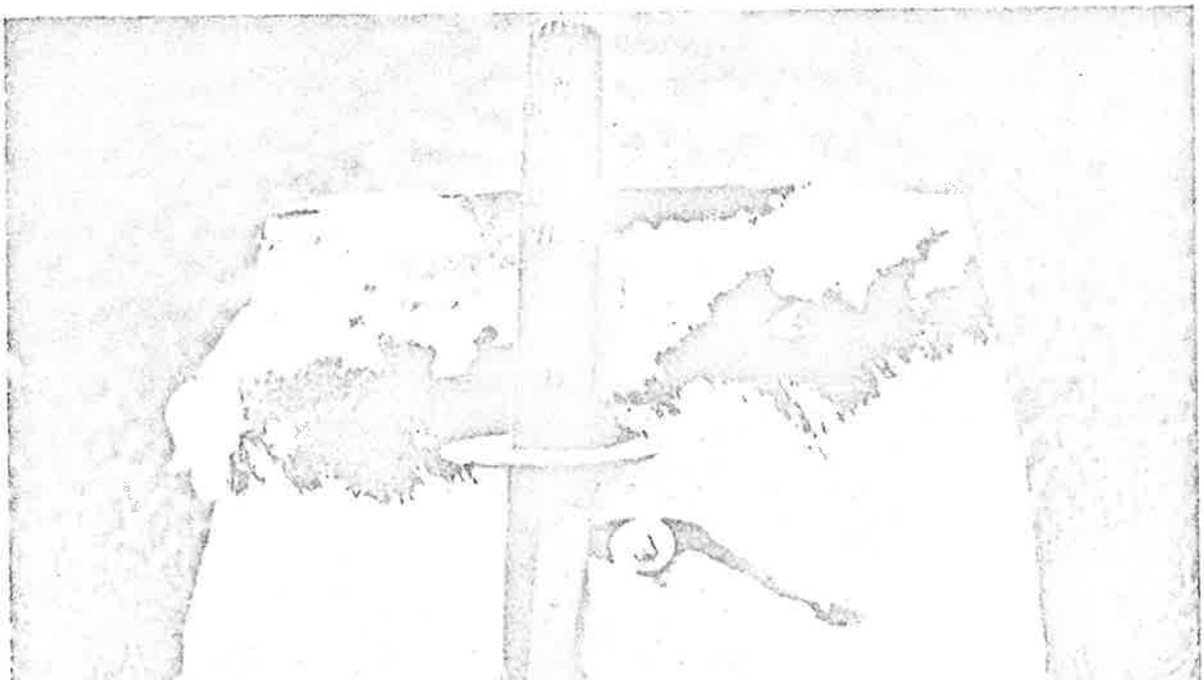

Figure 2. Stopper of modified mark number 11949, as if lodged in the blubber when fired into humpback body. The stoppers of the other three modified marks penetrated deeper into the blubber.

cies of whales, a smaller mark of less penetrating power might be suggested. Dr. D. E. Sergeant (Fisheries Research Board of Canada) is testing smaller marks of the same type as «Discovery» marks, for use upon smaller species of cetacea such as pilot whales *(Globicephala melaena)* and white whales *(Delphinapterus leucas)*. However, while smaller marks might be useful for the smaller species, when used upon humpbacks and other larger whales, the recovery rate for small marks would probably be even less than that of the «Discovery» mark. Omura and Kawakami (1956), have tested short marks in conjunction with attached nylon streamers, but have now reverted to the longer mark.

To improve the chances of recovery, some indi-ation should remain at or near the surface of the whale when marked. Dr. N. A. Mackintosh (personal ommunication) has suggested the use of a liquid stain in a plastic capsule which is punctured on impact. It has even been suggested that if a different oloured dye was used each year for calves only, an nternal mark may be unnecessary. Doan and ouglas (1953) experimented with a «tattoo» mark nvolving the injection of a distinctive dye pattern eneath the skin of white whales. The results of hese tests were inconclusive and the work has not een continued.

Modification of the «Discovery» mark.

In an effort to overcome the two major defi-iencies in the «Discovery» mark, the following modi-ication, shown in Figure 1, has been tested. The riginal mark was cut into two parts of equal ength. Between these two tubes was inserted a stopper» consisting of a smaller tube, 2.5 cms. long nd closed at one end. Around the middle of this topper a projecting collar, 3 mm. wide, increased the iameter to 1.85 cms. (just fitting freely into the bar-el of the marking gun). This stopper fitted rather irmly into the two shafts of the mark, with the pen end of the stopper at the front, and only the rojecting collar visible externally (upper mark in igure 1). The stopper was joined to the anterior haft of the mark by means of a stainless steel ingle strand wire, one metre long; coiled into a pring of 8 mm. diameter. There was no difficulty n fitting this length of wire into the anterior shaft, s a metre of the wire may be coiled into a spring nly 4 cms. long. The wires used in the tests were usic wires of diameters 0.38 mm. (approximately 3 gauge S.W.G.), 0.51 mm. (25 gauge S.W.G.), and 56 mm. (24 gauge S.W.G.).

For tests upon dead whales, the stopper was ade from brass rod. The stopper and wire increased the weight of the mark by 10 grams or approximately 15 %.

It is proposed that the anterior shaft and stopper be filled with a brilliant stain. If the stain is in the dry, powdered form, the weight of the mark would be increased as little as possible.

Such a modified mark is designed to operate in the following manner. As the mark forces through the fibrous blubber, the projecting collar halts the stopper near the skin while the anterior shaft (the mark proper) continues into the muscle, but is slowed down by the tissues closing over the partially expanded wire coil. Much of the stain would be pulled from the anterior shaft by the extension of the wire coil, and be distributed along the line of entry. The stain remaining in the stopper would slowly colour the surrounding blubber. The posterior shaft (only necessary to ensure a straight flight of the mark) might remain attached to the stopper and project from the surface of the body, but should soon work free and fall away, leaving the stopper in the blubber close to the skin. The anterior shaft, being embedded in the muscle, would help to anchor the stopper in the blubber. Being still partially coiled, the wire should not interfere too greatly in the freedom of movement of muscles beneath the blubber.

The potential advantages of such a modified mark are that the penetration of the shortened mark should be less than the original one (an advantage when marking calves), and that the blubber is distinctively coloured at the point of entry, thus increasing the chances of the mark being discovered at some later date. The stained blubber may not be readily visible externally because the dorsal skin of whales is generally black, but when flensing the stained area should be obvious on the undersurface of the blubber.

Trials with the modified mark.

In preliminary trials, four modified marks and three standard «Discovery» marks were fired into dead humpback whales at the Carnarvon whaling station (Nor' West Whaling Company), during September, 1956. No stain was placed in the modified marks as it was intended only to test the behaviour of the modification in operation, at a range similar to that used when marking at sea.

During December, two modified marks and two standard marks were fired into sperm whale carcasses at the Albany whaling station (Cheynes Beach Whaling Company). On this occasion the anterior shafts and stoppers of the modified marks were filled with stain. This consisted of equal parts of «lamp-black» (carbon) and waxoline rhodamine B.S., both in the dry, powdered form. Each mark held approximately 11 grams of the mixture.

Table 1. Results of Humpback whale marking trials at Carnarvon September, 1956.

Whale No.	Mark No.	Type of Mark	Marking distance (m)	Point of Entry	Result
973	11946	Standard	18	1 metre below dorsal fin.	Full penetration but oblique: point of mark 9 cms. into muscle.
974	11949	Modified: using 25 gauge wire.	18	1½ metres below and behind dorsal fin.	Oblique entry; posterior shaft of mark flew off at impact; stopper in blubber, projecting 0.4 cms. above skin; wire coil partly extended, not broken; point of mark 3½ cms. into muscle.
976	11944	Standard	18	1½ metres below and in front of dorsal fin.	Full penetration but oblique entry. Mark between blubber and muscle with point of mark 12 cms. into muscle.
976	11950	Modified: using 25 gauge wire.	18	30 cms. behind mark 11944.	Oblique entry; posterior shaft fell away, lying free on whale; stopper embedded in blubber, just visible from exterior; wire coil extended 15 cms. out of anterior shaft, not broken; point of mark 5 cms. into muscle.
998	11945	Standard	12	2 metres below and in front of dorsal fin.	Full penetration but oblique entry. Passed 18 cms. into muscle.
998	11947	Modified: using 28 gauge wire.	12	45 cms. behind mark 11945.	Oblique entry: posterior shaft remained attached to stopper, 7 cms. protruding from wound; stopper in centre of blubber; wire coil in half-circle through blubber to muscle, wire detached from stopper: anterior shaft completely embedded in muscle.
1000	11948	Modified: using 28 gauge wire.	16	1 metre below dorsal fin.	Mark entered at right angles to body surface; posterior shaft fell off; stopper embedded in blubber but could be touched by inserting finger into wound; wire coil still attached and not fully extended, coil passing through blubber in almost half circle; anterior shaft between blubber and muscle (tip 5 cms. into muscle), and lying at right angles to line of entry.

The results of these tests are summarized in Tables 1 and 2. It was perhaps unfortunate that the penetration both of standard and modified marks was not greater, so that a better comparison of depth could be made. In the tests upon humpback whales the relatively low penetration was probably largely due to the oblique angle at which the marks were fired. The construction of the whaling station made it difficult to effect shots at right angles to the body surface at these ranges. When fired into sperm whales, at right angles to the body surface, the penetration of marks was again not very great, in spite of the much closer range. This serves to emphasize the toughness of sperm whale blubber. Omura and Kawakami (loc. cit.) remark upon the tougher blubber of sperm whales in relation to marking.

The flight of the marks was little affected by the modification; modified marks embedded alongside standard marks at a range of 18 metres. The posterior shaft of the modified marks (only necessary to ensure straight flight of the mark) dislodged from the stopper on five occasions as the marks entered the whales. Although this may not be essential to the final success of the modified mark, it is preferable not to have a shaft projecting from the body as water flow upon this might tend to work the stopper out of the blubber. Also a projecting object tends to be scraped away as the whale is pulled up the slipway.

The stopper remained in the blubber in each of the six modified marks tested, while the anterior shaft penetrated more deeply. The stopper from mark number 11949 is shown in Figure 2 as it lodged in the blubber: the stoppers of the other marks tested were completely embedded in blubber beneath the skin.

In one modified mark the wire had parted from

Table 2. Results of Sperm whale marking trials at Albany, December, 1956.

hale No.	Mark No.	Type of Mark	Marking distance (m)	Point of Entry	Result
56	11940	Standard.	9	1½ metres behind head, dorsally.	Incomplete penetration although mark entered at right angles to body surface. Point of mark passed through 14 cms. of blubber, halting in muscle with 9 cms. of shaft still protruding from body. Shaft bent through 20 degrees at surface of blubber.
56	11941	Modified: using 24 gauge wire: carrying stain.	7.3	2½ metres behind head.	Anterior shaft penetrated 14 cms. of blubber and lodged completely in muscle with the point of mark 44 cms. from the skin (still vertical to body surface). Stopper embedded in blubber, the posterior surface 1 cm. below skin. Wire coil extended 28 cms. out of anterior shaft, not broken. Posterior shaft free of stopper, 2 cms. of its length loosely hanging in wound, and remaining 11 cms. protruding, bent through 45 degrees. Stain distributed from stopper to anterior shaft, along passage of mark.
60	11939	Standard	4.5	2 metres in front of and below dorsal fin.	Mark entered at right angles to body surface. Full penetration, but end of shaft only 5 mm. below surface of skin and visible in wound. Blubber thickness 11 cms. Mark slightly bent at junction of blubber and muscle.
60	11942	Modified: using 24 gauge wire: carrying stain.	4.5	30 cms. behind mark 11939.	Mark entered at right angles to body surface. Anterior shaft penetrated 10.5 cms. of blubber and lodged completely in muscle with point of mark 41.5 cms. from the skin. Stopper embedded in blubber, the posterior surface 2 cms. below skin. Wire coil extended approximately 27 cms. out of anterior shaft, not broken. Posterior shaft free of stopper, 1½ cms. of its length hanging loosely in wound, and remaining 11½ cms. protruding, bent through 40 degrees. Stain distributed from stopper to anterior shaft, along passage of mark.

stopper. In this case the thinner (28 gauge) e had been used. In future, stronger wire (24 ge S.W.G.) will be used.

Discussion.

In these trials the performance of the modified ks was considered satisfactory, and further elopment of this mark is planned.

It is possible that in a successfully marked le the continual movement of muscles beneath blubber during swimming motions might fa- e the wire so that it breaks at the junction of ber and muscle, resulting later in the loss of stopper. The coiling of the wire, allowing some tching with the muscles, should help to mini- e this. In any case, loss of the stopper after some e would not be so serious if the dye has stained surrounding blubber. Also the breaking of the wire does not mean that the all-important mark itself will be lost.

Obviously brass stoppers could not be used on living whales, owing to the toxicity of copper. The stopper can be produced in quantity from mild steel, at relatively low cost. A greater proportion of marks recovered, and the more valuable data obtained by marking whales of known age, would far outweigh the increased cost of such a modified mark.

The choice of a suitable stain presents some difficulties. The stain should be brilliant and permanent, but should not spread too far from the passage of the mark. Colloidal carbon remains localised very satisfactorily, so it is intended to use this with a brilliant stain of slight solubility, such as waxoline green G.S.

In conjunction with the development of this mark, some modification of the marking procedure is required. Instead of marking whales almost indiscriminately, it is suggested that future marking be confined where practical to the following, in order of priority:—

(a) Calves. As stressed earlier, the marking of these will yield invaluable information upon the growth rate, age, puberty, mortality, etc. as well as the usual data upon migration.

(b) Lactating females (parents of the above). These can be marked at the same time as the calves, and could considerably increase our knowledge of the rate of breeding in whales.

(c) «Yearling» whales still in company with their mothers. It has already been pointed out that there may sometimes be doubt as to whether a small whale in company with a larger one is a yearling or a two year old.

Acknowledgements.

The ready cooperation of the Nor' West Whaling Company and the Cheynes Beach Whaling Company in these marking trials is appreciated.

We are grateful to Mr. W. Jones (Instrument maker to the Department of Zoology, University of Western Australia) for carrying out the modifications to the marks.

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Paper 7

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Australian Marking of Humpback Whales

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I. INTRODUCTION

The objects and importance of whale marking in general are wellknown (Mackintosh 1952; Chittleborough and Godfrey 1957), and Dawbin (1956*a*) has stressed the importance of marking humpback whales, *Megaptera nodosa* (Bonnaterre) in the southern Pacific Ocean.

Since whale marking on the Australian Coast was commenced on a small scale in 1949 a considerable number of humpback whales have been marked and some useful recoveries made. In this report the results up to 1958 are summarized. This marking, which forms part of the programme of research upon the humpback whale, is being continued.

With the exception of five fin whales, *Balaenoptera physalus* (L), and one pilot whale, *Globicephala melaena* (Traill), which have been marked, whales marked in Australian waters are humpback whales.

II. HUMPBACK WHALES MARKED

After excluding all marks which either missed or ricochetted off whales, and also duplicate hits into the same whale, the numbers of humpback whales marked each year are recorded in Table 1. Whales from which the mark was recorded as protruding should not be regarded as successfully marked, as these marks would probably fall out within a short time. Marks recorded as «possible hits» have been recovered from whales in later years, and even one recorded as ricochet and one as missing the target, have later been found in whales. For this reason it is proposed to consider that one third of the possible hits resulted in successfully marked whales. By this means it is estimated from the results given in Table 1 that up to 1958 a total of 1019 humpback whales have been marked. Of these 786 were marked off the east coast of Australia, 16 off Norfolk Island, and 217 off the west coast of Australia.

When marking whales, it has been the practice to record an estimated length for each whale marked. However, from the lengths measured at the time of recapture (Table 2) it is evident that estimates of length at sea are of little real value unless the individual was especially small when marked.

At least 90 humpback whales were marked on the east coast of Australia with marks modified as described by Chittleborough and Godfrey (1957). Whenever possible females with young calves were marked; at least 67 lactating females and 37 calves have been marked. It was hoped that modified marks would prove less harmful to calves than the standard marks, but one calf marked with a modified mark was found dead some days later, approximately 250 miles south of the position when marked. From information supplied by the fishermen who returned this mark, it appeared that the mark had entered rather low in the body and pierced the intestines. It is expected that this would occur rarely.

Young calves proved difficult to mark, having surprising endurance, presenting a relatively small target for a shorter time than adults, and frequently surfacing on the side of the female away from the vessel.

When possible, preference was given to the marking of young whales, especially «yearlings» which reach Australian coasts in June (Chittleborough 1958). However, other work often made it necessary to defer marking until later in the year.

III. MARKS RECOVERED

Table 2 shows details of all marks recovered from humpback whales taken in Australian waters from 1951 to 1958. In 67 per cent. of these recoveries

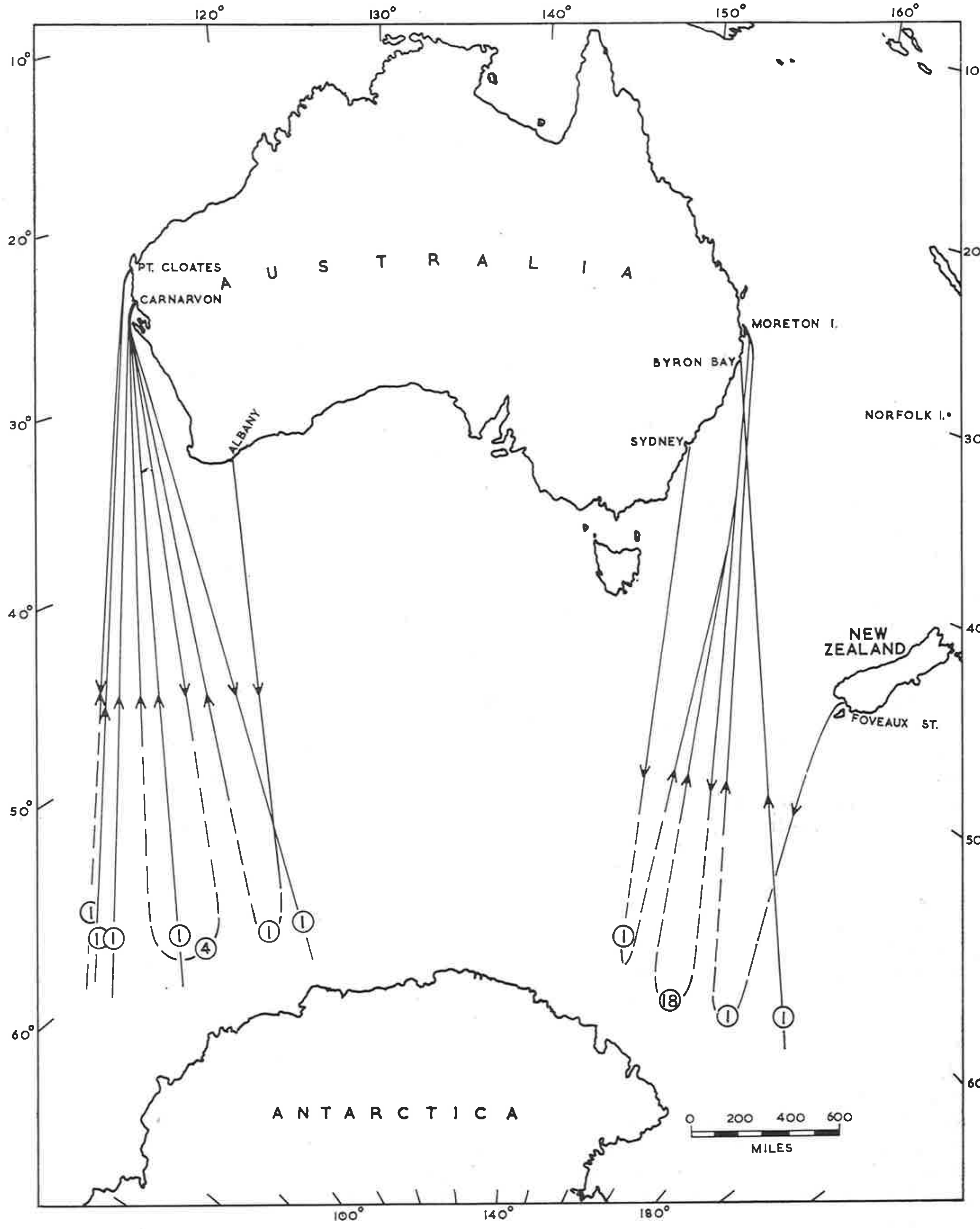

Fig. 1. Migrations of humpback whales.

it has been possible to identify the whale which had carried the mark, while the remainder of the marks were recovered from the cookers or in other parts of the factory. Ruud and Øynes (1954) also found that approximately one third of recovered marks were found in the cookers. One whale on the east coast of Australia was marked three times and shot by a catching vessel later in the same day. The mark which had been recorded as protruding was recovered during flensing operations, but the two marks which had penetrated deeper were found some days later when residues were being moved from the cookers.

In addition to the recoveries listed in Table 2, two Australian marks have been recovered in other regions. Mark No. A188 was fired into a humpback whale off the west coast of Australia and recovered six months later in Area IV of the Antarctic (Brown 1956), while mark No. 16471 was fired off the east coast of Australia and recovered twelve months later in New Zealand (Dawbin 1959).

Table 3 shows the intervals which had elapsed between firing and recovery of Australian marks. Although the number of marks recovered is not yet very large, similar numbers were taken after one, two, and three years, indicating that the whales make the winter migration every year. Recoveries have been very erratic; for example, although far more humpback whales were marked in 1956 than in 1955 (Table 1), the annual recovery rate has been lower from the former group than from the latter.

IV. MIGRATIONS OF MARKED WHALES

Figure 1 shows the migrations of humpback whales as indicated from recent recoveries of marks in Australian waters and of one Australian mark recovered in the Antarctic. The four Russian marks recovered at Carnarvon in 1958 are not shown as details of their firing have not yet been received. Migrations are indicated by straight lines: obviously the actual paths would have been influenced by coastlines and food supply. The probable migrations of individuals marked in temperate waters and recaptured one or more years later in temperate waters are shown by broken lines.

It can be seen from Figure 1 that no interchange between the Group IV (longitude 70° E. to 130° E.) and the Group V (longitude 130° E. to 170° W.) populations has yet been recorded.

The movements of marked whales between the west coast of Australia and Antarctic Area IV confirm the known migration of humpback whales in this population (Raynor 1940).

Another link between humpback whales of Antarctic Area IV and the west coast of Australia was established in a unique manner. On January 29, 1954, a member of a whaling expedition threw into the Southern Ocean a dentifrice tin containing a message bearing his name and address. The position of the vessel was then close to 64½° S., 92° E. On June 27, 1954, this tin and message was recovered from the intestines of a humpback whale which was being processed at the land station near Albany, Western Australia.

The recovery in June, 1958, from the east coast of Australia of a mark from a humpback whale marked in Antarctic Area V gives the first confirmation of the postulated migrations of humpback whales within the Group V stock (see Mackintosh 1942).

Nineteen marks recovered on the east coast of Australia had been fired into humpback whales along the same coastline one to three years earlier, while one whale marked in Foveaux Strait, New Zealand, during a southward migration was killed nine months later on the east coast of Australia. It would appear that within the Group V population individuals tend to follow the same migration path each year, but that after mingling in the one Antarctic feeding area, some individuals change from one migration route to another.

Further information upon the migrations and dispersal of humpback whales of the Group V population has been obtained from the widespread marking programme organized by W. H. Dawbin (1959). More detailed information upon this aspect may be anticipated as increasing numbers of marks are recovered from this population.

V. OTHER INFORMATION FROM MARKED WHALES

Although short-term recoveries of marks within a few days of marking are usually of little value, they may sometimes yield information upon the rate of movement of whales. For example, mark No. A137 was fired into a humpback whale on the east coast of Australia in 1953 during the northward migration, and when recovered six days later had travelled at least 520 nautical miles, giving an average speed of 3.6 knots. Mark No. A236 was fired into another humpback whale in similar circumstances in 1958 and recovered seven days later after travelling at least 430 n. miles northward, giving an average speed of just over 2.5 knots. These rates of travel are similar to those reported by Chittleborough (1953) for humpback whales kept under direct observation for short periods during undisturbed northward migrations. However Dawbin (1956*b*) by comparing the times when the bulk of the humpback whales pass separate points on a migration route, has indicated that the average rate of progression of migrating humpback whales is close to 1.3 knots.

Nine humpback whales marked on the east coast of Australia during June and early July (during the northbound migration) of either 1955 or 1956, were killed in the same locality in 1958 in the same months, but in all cases the dates of killing were a few days later than the dates of marking in the earlier years. The differences between the dates varied from five to fifteen days, with a mean of 8.8 days. This could indicate that the northward migration in 1958 was slightly later than in 1955 or 1956. Dawbin (1956*b*, Fig. 4) has clearly shown annual variations in the time of the northward migration of humpback whales passing through Cook Strait, New Zealand.

Recoveries of marks from female whales which had been marked in previous years when accompanied by a calf can yield useful information upon the rate of ovulation and breeding of females if the whales have been adequately examined when the marks were recovered. Two such recoveries have been made on the Australian coast and are described elsewhere (Chittleborough 1959).

It is hoped that later recoveries of marks from whales marked when young will enable present methods of age determination to be checked. Some such recoveries have been reported from New Zealand (see Dawbin 1959).

VI. ACKNOWLEDGEMENTS

The National Institute of Oceanography (England) has been most helpful in the supply of whale marks for this work and in the exchange of information upon marks fired or recovered in the Antarctic.

The assistance of the State Fisheries Department of Western Australia in making one of its vessels available for marking on the west coast is gratefully acknowledged.

Australian whaling companies have been cooperative in the return of marks recovered. State and Commonwealth Whaling Inspectors have also been helpful in furnishing details of marks recovered.

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Table 1.
Humpback Whales marked in Australian Waters 1949/1958

Year	East Coast			West Coast			Norfolk Island	
	Fully Marked	Possible Mark	Mark Protruding	Fully Marked	Possible Mark	Mark Protruding	Fully Marked	Possible Mark
1949				15	1	4		
1950	4							
1951								
1952	4							
1953	14		2					
1954	59	7	4	20	1	1		
1955	161	19	3	53	16	1		
1956	364	12	11	6			14	3
1957	51	12	3	70	10	4	1	2
1958	109	9	4	41	7	2		

Table 2.
Marks recovered from Humpback whales in Australian Waters 1951—1958.

Mark Number	Release			Recovery		
	Date	Position	Remarks	Date	Position	Remarks
A15	1.8.49	23°31'S. 113°27'E.	Female with calf	5.7.58	25°31'S. 112°45'E.	Female 43 ft 6 in. 10 corpora albicantia
A20	2.8.49	22°37'S. 113°36'E.		5.10.51	22°38½'S. 113°39'E.	Female 42 ft 3 in.
A32	16.7.55	24°40'S. 113°25'E.	Adult	18.7.55	25°00'S. 113°23'E.	Male 40 ft
A99	17.8.54	35°02'S. 118°08'E.	Female with young calf	22.9.56	25°59'S. 113°00'E.	Female 40 ft 3 corpora albicantia
A120	11.6.53	35°20'S. 150°30'E.		6.8.56	Moreton I. 27°11'S. 153°24'E.	Found in grax pump
A137	7.7.53	35°10'S. 150°45'E.		13.7.53	27°00'S. 153°26'E.	Male 43 ft
A236	4.7.58	34°0'S. 151°16'E.	Approx. 39 ft	11.7.58	27°05'S. 153°29'E.	Female 45 ft 8 in.
5136	29.1.36	60°01'S. 88°55'E.		26.7.53	22°38'S. 113°39'E.	? Female 46 ft 7 in. 14 corpora albicantia
5202	1.1.36	61°00'S. 90°32'E.	Recorded as ricochet	8.10.51	Carnarvon	Found in cooker
11690	6.10.54	Off Moreton I. approx. 27°S. 153½°E.	Approx. 38 ft	23.7.55	27°08'S. 153°28'E.	Female 41 ft
11692	6.10.54	Off Moreton I.	Approx. 42 ft	18.10.54	Byron Bay. 28°37'S. 153°38'E.	Found in cookers
11730	7.10.54	Off Moreton I.	Approx. 40 ft	19.6.56	27°05'S. 153°29'E.	Male 39 ft
11738	8.10.54	Off Moreton I.	Approx. 38 ft	13.6.56	27°04'S. 153°29'E.	Female 39 ft 10 in.
11746	23.6.55	Off Moreton I.	Approx. 40 ft	16.6.56	27°15'S. 153°33'E.	Male 38 ft 9 in.
11752	23.6.55	Off Moreton I.	Approx. 38 ft	28.6.58	26°58'S. 153°28'E.	Male 40 ft
11770	27.6.55	Off Moreton I.	Approx. 40 ft	7.8.58	Moreton I.	Found in separator tank
11774	27.6.55	Off Moreton I.	Approx. 40 ft	6.7.57	26°59'S. 153°26'E.	Male 38 ft 9 in.
11786	28.6.55	Off Moreton I.	Approx. 36 ft	4.7.58	27°06'S. 153°30'E.	Male 40 ft 10 in.
11788	28.6.55	Off Moreton I.	Approx. 41 ft	Aug.1958	Moreton I.	Found in cooker
11804	28.6.55	Off Moreton I.	Approx. 40 ft	13.7.58	28°38'S. 153°42'E.	Male 45 ft 8 in.
11808	29.6.55	Off Moreton I.	Approx. 40 ft	4.7.58	27°01'S. 153°29'E.	Male 39 ft 6 in.
11834	5.7.55	Off Moreton I.	Approx. 38 ft	20.6.56	27°03'S. 153°30'E.	Male 39 ft 5 in.
11835	5.7.55	Off Moreton I.	Approx. 40 ft	12.7.58	28°37'S. 153°41'E.	Male 40 ft 10 in.
11840	5.7.55	Off Moreton I.	Approx. 35 ft Recorded as possible hit	18.7.58	Moreton I. 27°11'S. 153°24'E.	Found in cookers
11853	7.7.55	Off Moreton I.	Approx. 39 ft	7.7.55	27°02'S. 153°30'E.	Male 39 ft
11884	14.7.55	Off Heron I. 23°30'S. 151°56'E.	Approx. 40 ft	10.8.56	Moreton I.	Male 40 ft 7 in.
11903	27.7.55	24°54'S. 113°17'E.	Approx. 40 ft	20.10.58	Carnarvon	Found in cooker at end of season
11909	2.8.55	25°30'S 113°03'E.	Approx. 34 ft	14.6.57	Carnarvon 24°53'S. 113°38'E.	Male 38 ft
11963	18.7.55	Off Moreton I.	Approx. 40 ft	1.8.58	26°59'S. 153°26'E.	Male 43 ft 8 in.
11986	24.7.55	Off Moreton I.	Approx. 37 ft	24.7.55	26°57'S. 153°30'E.	Female 37 ft 8 in. Mark protruding
11987	24.7.55	Off Moreton I.	Same whale as 11986	Aug.1955	Moreton I.	Found in cookers
11988	24.7.55	Off Moreton I.	Same whale as 11987	Aug.1955	Moreton I.	Found in cookers

Mark Number	Release			Recovery		
	Date	Position	Remarks	Date	Position	Remarks
12127	26.7.55	Off Moreton I.	Approx. 40 ft	31.7.55	Byron Bay	Found in cooker
13781	Feb.1955	63°14'S. 98°10'E.		24.6.57	25°35'S. 113°15'E.	Male 38 ft
14309	13.9.56	Off Norfolk I. 25°S. 167°85'E.	Approx. 38 ft	13.9.56	Norfolk I.	Male 36 ft 5 in.
16392	21.9.57	Shark Bay c. 25° S. 113°15'E.	Adult with calf	8.9.58	Carnarvon	Found in cooker
16729	3.7.56	Off Moreton I.	Approx. 38 ft	10.7.58	27°09'S. 153°31'E.	Male 46 ft 2 in.
16866	9.7.56	Off Moreton I.	Recorded as miss	16.7.58	Moreton I.	Found in cooker
17236	5.11.57	Foveaux Str. N.Z. 47°S. 168½°E.	Approx. 40 ft	5.8.58	27°06'S. 153°29'E.	Female 42 ft 10 in.
19504	18.9.57	Off Moreton I.	Calf under 20 ft	c.1.10.57	31°49'S. 152°45'E.	Washed ashore
19934	27.12.57	65°49'S 179°45'E.		27.6.58	28°38'S. 153°43'E.	Male 43 ft 6 in.
1007 U.S.S.R.	Information not yet available			4.9.58	Carnarvon	Found in cooker
1027 U.S.S.R.				8.9.58	Carnarvon	Found in cooker
1030 U.S.S.R.				4.9.58	24°39'S. 112°57'E.	Female 40 ft 9 in. 1 corpus albicans
1165 U.S.S.R.				8.9.58	Carnarvon	Found in cooker

Table 3.

Intervals between Release and Recovery of Marks: Humpback Whales marked in Australian Waters.

Year Marked	Interval until Recorded					
	0 yrs	½ yr	1 yr	2 yrs	3 yrs	9 yrs
1949				1		1
1950						
1951						
1952						
1953	1				1	
1954	1		1	3		
1955	6	1	3	2	10	
1956	1		1	2		
1957	1		1			
1958	1					
Total	11	1	6	8	11	1

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Paper 8

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Intermingling of two Populations of Humpback Whales

By R. G. Chittleborough

Intermingling of two Populations of Humpback Whales

By R. G. Chittleborough*)

I. Introduction.

Catches and observations of humpback whales, *Megaptera nodosa* (Bonnaterre), in Antarctic waters show that these whales tend to gather in relatively distinct feeding concentrations during the summer months (Mackintosh 1942). The areas within which these concentrations occur have been delineated: those whales occurring between longitude 70°E. and 130°E. are known as Group IV, while humpbacks located between the longitude of 130°E. and 170°W. are known as the Group V population. The corresponding sectors of Antarctic waters are known as Antarctic Areas IV and V respectively.

Mackintosh and others have shown that within Antarctic Area IV the greatest concentration of humpback whales occurs (during the summer) between 80°E. and 100°E. Whale marking (Rayner 1940; Chittleborough 1959*a*) has shown conclusively that these whales migrate to the west coast of Australia during the winter.

Recent recoveries of whale marks (Chittleborough 1959*a*; Dawbin 1959) have verified earlier assumptions that humpback whales which feed in Antarctic Area V during the summer migrate to the east coast of Australia and to the south-west Pacific islands during the winter.

Until this year no evidence had been found of any interchange between the Group IV and Group V populations of humpback whales and it has become customary (see Chittleborough 1958) to regard catches from either Area as being composed entirely of individuals from that particular population. Analysis of catch returns of humpback whales taken in Antarctic Areas IV and V during February 1959, supplemented by recoveries of whale marks during the same period, shows that this assumption must now be revised.

II. Analysis of Catches made in Antarctic Areas IV and V during 1959.

During the Antarctic whaling season in the summer of 1958/59, the hunting of humpback whales was permitted only during the first four days of February. Details of catches forwarded to the Bureau of International Whaling Statistics show that a total of 1796 humpback whales was taken from Antarctic Area IV and 502 from Antarctic Area V during this period. The distribution of these catches, grouped in 5° intervals of longitude, is shown in Figure 1. It is seen that a large sample (1029 individuals) was taken from the western portion of Antarctic Area IV (from 75°E. to 99°E. longitude), another sample (767 individuals) from the eastern portion of this sector (from 110°E. to 130°E. longitude), while a slightly smaller sample (502 individuals) was obtained from almost the centre of Antarctic Area V (from 155°E. to 169°E.). For convenience these three samples will be referred to as A, B, and C, respectively.

It is realized that the sizes and distribution of these samples may be largely due to the location of factory ships during the short catching period and the catches are therefore not necessarily a proper indication of the distribution and relative abundance of humpback whales at that time. However, these three geographically separated samples are sufficiently large to be analysed separately in order to compare the composition of the catches made in each region.

Figure 2 shows the length frequency distribution for the males in each of the three samples. The

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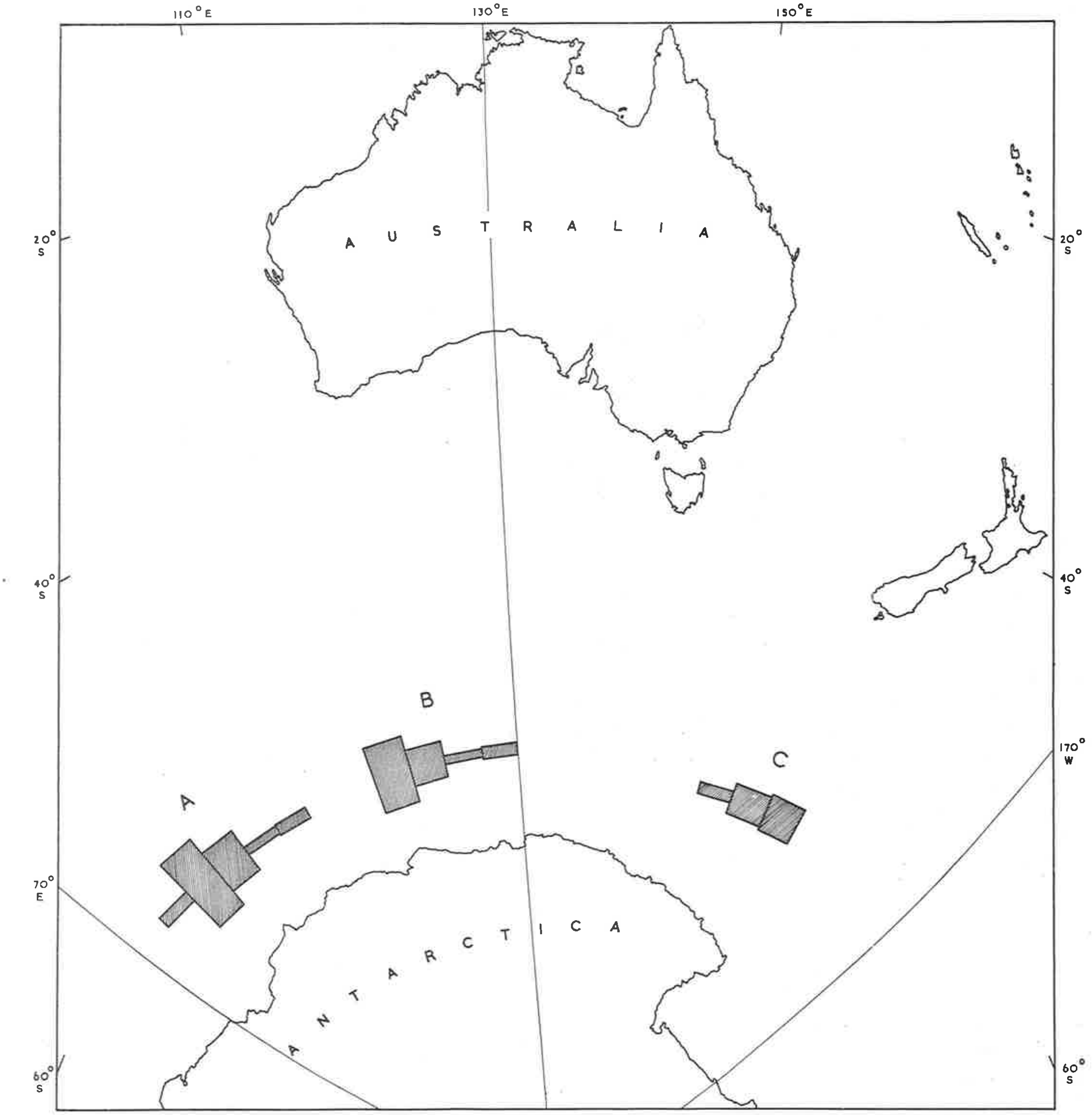

Fig. 1. — Location of catches of humpback whales taken from Antarctic Areas IV and V during February, 1959, in 5° intervals of longitude. Heights of each column indicate relative numbers taken.

catch of males within sample A differed greatly from that in sample C, the former being composed of smaller individuals than the latter. The lengths of the males taken from the intermediate region (sample B) were distributed between those of the two adjacent samples.

The mean lengths and percentages of sexually immature individuals for the male humpback whales taken in the three regions are given in Table 1. The percentages of immature males were estimated by classing all males of less than 37 feet in length as immature (see Chittleborough 1958). Table 1 shows that in these three samples the mean lengths of the males increased progressively from west to east, while the percentage of immature males decreased from west to east.

Figure 3 shows the length frequency distribution for the females in each of the three samples. This shows that the catch of females within sample A was composed of smaller individuals than in either sample B or C. The mean lengths and percentages of immature individuals for the females taken in the three localities are given in Table 1. The percentages of immature females were estimated by classing all females of less than 39 feet in length as immature (see Chittleborough 1958). Table 1 shows that while the mean lengths of females in samples B and C were similar, the mean length of the females taken from sample A was considerably less than in the two former samples. The percentages of immature females decreased progressively in the samples from west to east, as in the case of the immature males.

Table 2 summarizes the results of comparisons of the mean lengths of samples of humpback whales taken during February 1959 from the three localities under discussion. This shows that except in the comparison of the females in sample B with those females in sample C the mean lengths of both males and females differed significantly (1 % level) from one region to another. Thus it is highly improbable that the differences shown between the three samples could have resulted from random sampling within one uniformly distributed population of humpback whales.

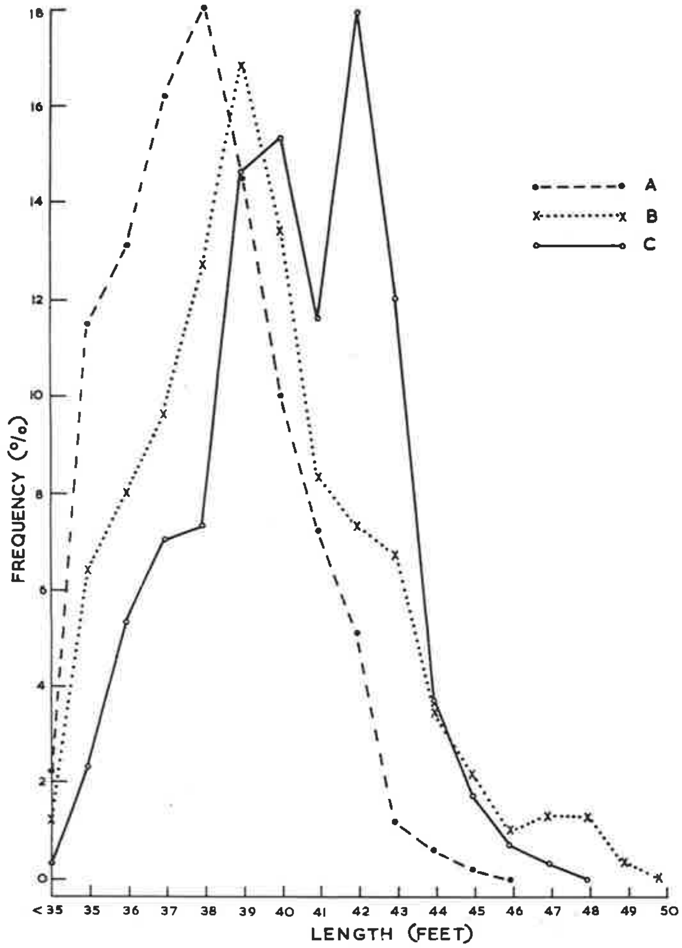

Fig. 2. — Length frequency distribution of male humpback whales taken in three regions of the Antarctic during February, 1959.

III. Marks recovered from Humpback Whales in Groups IV and V.

Rayner (1948) has given the positions of approximately 400 whale marks fired into humpback whales from 1934 to 1937 in Antarctic Area IV. This marking was carried out in the western part of Area IV, from 75°E. to 102°E. longitude, the majority of the whales being marked in the region from 85°E. to 99°E. longitude where a concentration of humpback whales was reported. Up to 1938, Rayner (1940) recorded the recovery of 22 of these marks from humpbacks taken on the west coast of Australia. Two more of these marks have been recovered on the west coast of Australia in recent years (Chittleborough 1959*a*). Another mark, fired into a humpback whale in the western portion of Antarctic Area IV (98°10'E.) during February 1955, has also been recovered on the west coast of Australia (see Chittleborough 1959*a*).

In addition to the above, details now received show that four Russian whale marks recovered on the west coast of Australia in September 1958 (see Chittleborough 1959*a*) had been fired into humpback whales during February 1958 near 63°S. 95°E.

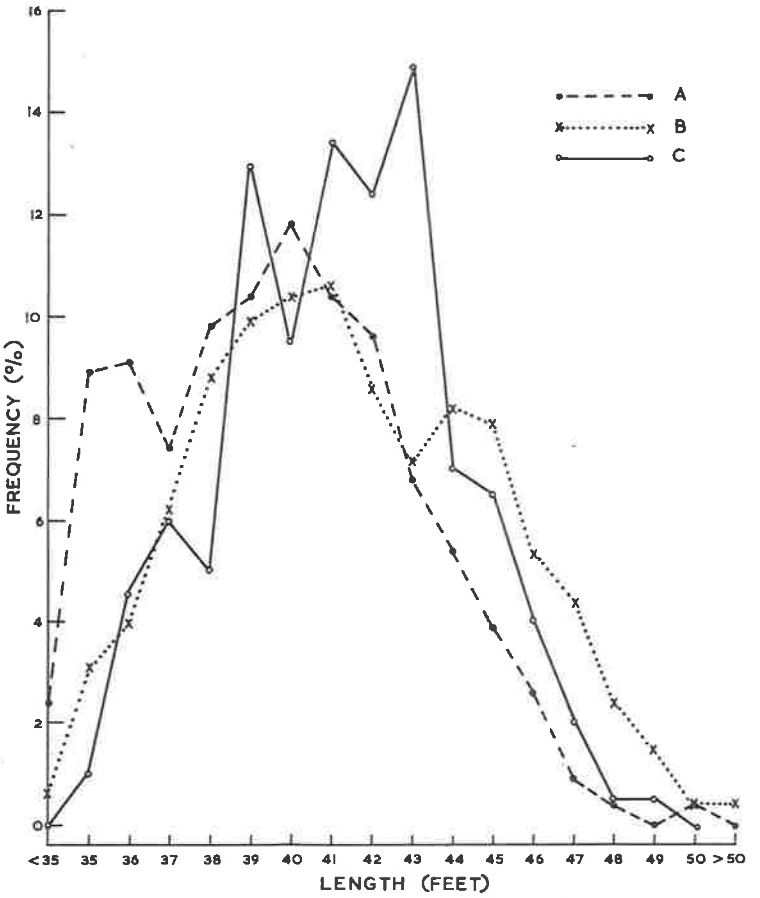

Fig. 3. — Length frequency distribution of female humpback whales taken in three regions at the Antarctic during February, 1959.

These recoveries of whale marks demonstrate conclusively that the concentration of humpback whales which spent the summer in the western portion of Antarctic Area IV migrated to the west coast of Australia for the winter months.

Less is known of the movements of humpback whales which have been found in the eastern portion of Antarctic Area IV during the summer, but the recovery of a mark, fired into a humpback off the west coast of Australia, from a whale shot at 114°32'E. longitude in the Antarctic during February 1956 (see Brown 1956) linked the humpback whales found in the eastern portion of Antarctic Area IV with those spending the winter months off the west coast of Australia.

The recovery on the east coast of Australia of a mark fired into a humpback whale in Antarctic Area V (Chittleborough 1959*a*), and the recovery at Tonga of two marks also fired into a humpback in Antarctic Area V (Dawbin 1959) showed that humpbacks found in Antarctic Area V during the summer migrated to the east coast of Australia and to the south-west Pacific islands during the winter.

The recoveries of marks from humpback whales taken in Antarctic Areas IV and V during February 1959 yield fresh information on the movements of humpback whales and this information is relevant to the analysis of the catches made in those areas at that time. The National Institute of Oceanography has notified that eleven Australian whale marks, one New Zealand mark, and four marks fired in Antarctic Area V, were recovered from humpback whales taken in the Antarctic during February 1959. The catch of humpbacks made in the western part of Antarctic Area IV (75°E. — 99°E. longitude) resulted in the recovery of one mark which had been fired off the west coast of Australia. The humpbacks taken in the eastern portion of Antarctic Area IV (110°E. — 130°E.) yielded one mark fired off the west coast of Australia, six marks fired off the east coast of Australia, and two marks fired in previous years in Antarctic Area V. From the catch made near the centre of Antarctic Area V (155°E. — 169°E.) six marks were recovered. Three of these had been fired off the east coast of Australia, one off the coast of New Zealand, and two in Antarctic Area V.

Table 1.

Analyses of Catches of Humpback Whales taken in Antarctic Areas IV and V during February 1959.

Males

Location (Longitude)	Number taken	Mean length (ft)	Standard deviation of mean	Immature %
75°— 99°E.	488	37.98	0.24	26.8
110°—130°E.	314	39.52	0.51	15.6
155°—169°E.	301	40.28	0.34	8.0

Females

Location (Longitude)	Number taken	Mean length (ft)	Standard deviation of mean	Immature %
75°— 99°E.	541	39.65	0.50	37.5
110°—130°E.	453	41.45	0.61	22.7
155°—169°E.	201	41.26	0.57	16.4

Table 2.

Comparison of mean Lengths of Samples of Humpback Whales taken in February 1959 from Regions A (75°—99°E.), B (110°—130°E.), and C (155°—169°E.).

Males			*Females*		
Samples compared	«t» value	Degrees of freedom	Samples compared	«t» value	Degrees of freedom
A, C	13.42	787	A, C	5.95	740
A, B	8.20	800	A, B	8.09	992
B, C	3.44	613	B, C	0.68	652

IV. Discussion.

The catches of humpback whales taken in the three separate regions within Antarctic Areas IV and V during 1959 were each taken during the same short period (of four days duration) and were of sufficient magnitude to assume that selection by gunners was at a minimum. Therefore it is highly likely that the catches in the three regions were representative of the whales available within each locality at that time.

In each of the features considered the catches of both males and females taken in the western portion of Antarctic Area IV (75°E. to 99°E. longitude) differed markedly from the sample taken in Antarctic Area V (in the region from 155°E. to 169°E.). The catch in the former region (sample A) had significantly lower mean lengths and higher percentages of immature individuals than sample C (from 155°E. to 169°E.). These differences are consistent with previous evidence (Chittleborough 1958, 1959*b*, *c*) of a recent decline in that population of humpback whales which migrates to the west coast of Australia each winter.

In size composition and percentages of immature individuals, the catch of humpback whales taken between 110°E. and 130°E. was intermediate between the catches made in the adjacent regions (75°—99°E. and 155°—169°E.). From this it is inferred that the sample taken between 110°E. and

Table 3.

Recent Catches of Humpback Whales from the Antarctic from Longitude 70°E. to 150°W.

Longitude:	Numbers of Humpback Whales Taken						
	1958—59	1955—56	1953—54	1952—53	1951—52	1950—51	1949—50
70— 74°E					103		
75— 79°E	76	118		2		5	
80— 84°E	534	214			60	37	31
85— 89°E	295	56			207	313	482
90— 94°E	50		258				47
95— 99°E	74	2		191		597	
100—104°E					219	160	22
105—109°E					137		78
110—114°E	429	262					2
115—119°E	225	180			169		8
120—124°E	42				232		61
125—129°E	71						48
130—134°E							12
135—139°E							18
140—144°E							7
145—149°E		40					730
150—154°E		105					132
155—159°E	81	49					4
160—164°E	197						
165—169°E	224			161	70		
170—174°E				68	38		
175—179°E				141	2	84	
180—176°W					36	15	
175—171°W				134		63	
170—166°W		148	14			2	
165—161°W		110	114	12	37	64	
160—156°W		15	22				
155—151°W							

130°E. was composed of a mixture of the Group IV and Group V populations. This is confirmed by the recovery within this region of whale marks from both the west and east coasts of Australia. It may be only by chance that the ratio of Australian marks recovered in this mixed sample was one west coast to six east coast marks, but from the comparison of the catches made in the three regions of the Antarctic (Figs. 2 and 3, Tables 1 and 2), it is probable that more than half of the whales sampled in the region from 110°E. to 130°E. were from the Group V stock of humpback whales.

In the comparison of the composition of the catches made in the three regions of the Antarctic during 1959, the evidence of intermingling of the two populations is clearer in the case of the males than in the females. This is because, as previously shown (Chittleborough 1959*b*), within the Group IV stock the males have been more severely depleted than the females.

Since there was a considerable movement of humpback whales from the Group V population into the eastern portion of Antarctic Area IV during the summer of 1958/59, the catches of earlier years were examined for similar evidence. Table 3 gives the distribution of catches of humpbacks taken in the Antarctic from 70°E. longitude eastwards to 150°W. for each year since 1949, the catches being shown as totals within each 5° interval of longitude. Once again it should be stressed that the location of catches tends to reflect the positions of factory ships in the limited catching periods allowed for humpback whales, rather than being a true indication of the distribution and relative abundance of this species.

Table 3 shows that within Antarctic Area IV catches of humpbacks in recent years have tended to be higher toward the western part of this area. In the summer of 1949/50 catches of humpbacks were distributed almost continuously from 80°E. to 154°E., but the relatively low numbers taken from 90°E. to 145°E. might indicate that no concentration of humpback whales was found in this region at that time.

Catches of humpbacks in Antarctic Area IV during February 1956 were similarly distributed (but of smaller magnitude) to those made in February 1959, but the mean lengths of both males and females taken from 75°E. to 99°E. in February 1956 did not differ significantly from the mean lengths of males and females taken from 110°E. to 120°E. during the same period. It may be significant that the only Australian whale mark recovered from the eastern part of Antarctic Area IV during 1956 was from the west coast of Australia.

Although the material is inadequate for a complete investigation of this aspect, the available data show no evidence of any significant mingling of Group IV and Group V populations of humpback whales prior to 1959.

At present there is no information to explain why there should have been an apparently large influx of Group V humpback whales into the eastern portion of Antarctic Area IV during the summer of 1958/59, but it seems reasonable to suggest that an environmental change (possibly of a temporary nature) resulted in some change in the distribution of euphausiids, enabling the humpback whales in the Group V population to feed farther west than usual.

It does not follow that humpback whales from the Group V population may be expected to be taken during the winter of 1959 on the west coast of Australia, as those from the Group V stock which fed in the eastern part of Antarctic Area IV might well have returned to Antarctic Area V before migrating northwards in the autumn. However, the large scale intermingling of two populations of humpback whales in the Antarctic during the summer of 1958/59 shows that catches within one of the somewhat arbitrarily defined areas of the Antarctic can no longer be automatically regarded as typifying a particular population of humpback whales.

V. Acknowledgments.

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I am grateful also to the National Institute of Oceanography, England, for forwarding details of whale marks recovered from the Antarctic.

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Paper 9

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DETERMINATION OF AGE IN THE HUMPBACK WHALE, *MEGAPTERA NODOSA* (BONNATERRE)

By R. G. Chittleborough

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Summary

The use of baleen, ear plugs, and ovaries in the determination of age in humpback whales is described.

From the evidence of baleen, the majority of humpback whales reach puberty at 4 or 5 years of age.

The rate of accumulation of laminations in ear plugs is two laminations per year. The mean rate of ovulation in sexually mature females is 1·1 per year. Age determination upon the same sample of mature females by these two methods gives very similar distribution of ages.

The age distribution within separate sexes from samples of mature humpback whales examined on the west and east coasts of Australia in 1957 are compared. The results indicate that the population migrating along the west coast is at present composed of younger individuals than that on the east coast of Australia.

I. Introduction

In a study of whale populations it is necessary to determine the ages of individuals and so obtain the age distribution within samples of these populations.

One of the methods of age determination which showed promise in earlier investigations was the number of ovulations in mature female whales. Mackintosh and Wheeler (1929) pointed out that corpora albicantia appear to persist for a considerable time in the ovaries of whales, the numbers of corpora albicantia being much higher in large physically mature females than in smaller females. It has since been shown (Laws 1958) that corpora albicantia, after some involution, remain in the ovaries of whales as recognizable bodies. Then if the age at puberty and the mean rate of ovulation have been determined for a particular species of whale, the approximate ages of mature females can be calculated.

Various estimates have been made of the rate of ovulation in blue and fin whales (see Nishiwaki 1952; Laws 1958) but this method has not yet been studied intensively in the case of the humpback whale, *Megaptera nodosa* (Bonnaterre). From limited data, Matthews (1937) suggested an average of five ovulations for each 2-year breeding cycle (succeeding the first sexual cycle) in the female humpback whale, but more recent work (Chittleborough 1954) showed this estimate to be too high.

Another useful method of age determination in the Mysticeti was discovered by Ruud (1940) of Norway and independently by Tomilin in Russia (see Ruud 1950). This is based upon periodic growth of the cortical layers in the baleen, as

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shown by seasonal variations in the total thickness of the baleen plate. Age determination from baleen plates has been studied extensively in blue and fin whales (Ruud 1945, 1950, 1955; Ruud, Jonsgård, and Ottestad 1950; Nishiwaki 1952; Hylen, Jonsgård, Pike, and Ruud 1955) but has not yet been applied to humpback whales although seasonal variations in thickness of baleen plates have been demonstrated in this species.

An advantage in using baleen rather than ovaries is that the former method is applicable to both sexes. Unfortunately wear at the free end of baleen plates restricts this technique to the younger individuals.

The recent discovery by Purves (1955) of laminations within the core of ear plugs affords a very promising method of age determination in the Mysticeti, applicable to both sexes and individuals of all ages. This method has been applied to small samples of fin whales (Laws and Purves 1956; Nishiwaki 1957) and humpback whales (Symons and Weston 1958). Assuming two laminations to be laid down in the ear plugs each year, fair agreement was found in ages estimated from ear plugs and from baleen.

In this paper ovulation counts, baleen traces, and ear plug laminations are used for the determination of age in humpback whales. The relationships between these methods are investigated. Mortality curves obtained from samples of two populations of the humpback whale are compared.

II. MATERIAL

Baleen traces were obtained from 629 humpback whales (238 males, 391 females) and ear plugs from 657 individuals (370 males, 287 females). In each case the gonads were collected and examined. Some additional baleen samples and ear plugs were collected but not used owing to damage or because of doubtful interpretation. Baleen or ear plugs collected without corresponding gonad data have also been rejected. The material was collected at shore-based whaling stations on the west and east coasts of Australia.

III. INTERPRETATION OF MATERIAL

(a) *Ovaries*

The examination of ovaries has already been described (Chittleborough 1954). As previously stated (Chittleborough 1955*b*) mature female humpback whales taken in Australian waters may have recently ovulated or may be killed during prooestrus. In order to apply a uniform standard in age determination from ovarian data it is intended to consider only the ovulations which had occurred in seasons prior to that of killing. These previous ovulations may be represented either by corpora albicantia alone or may include the corpus graviditatum of females in very advanced pregnancy (as this body represents an ovulation in the previous winter).

(b) *Baleen*

Traces were obtained from strips of baleen passed through a recording apparatus constructed from the description given by Ruud (1940). One of the longest baleen plates from each whale was used and care was taken to ensure that the trace was obtained from the gum to the tip of the plate, following a line parallel to the longitudinal fibres within the plate. The portion of baleen which is embedded in the gum is not shown by this method.

In the interpretation of baleen traces from humpback whales it was found that the majority of the traces could be separated into seven typical patterns which are illustrated in Figure 1, the examples given being copies of actual baleen traces. When considering individuals in each of these groups, ovarian and ear plug data showed that the sixth and seventh group were not each of one age class but contained individuals of widely varying ages. For this reason these two baleen groups have been merged into one age group (6+).

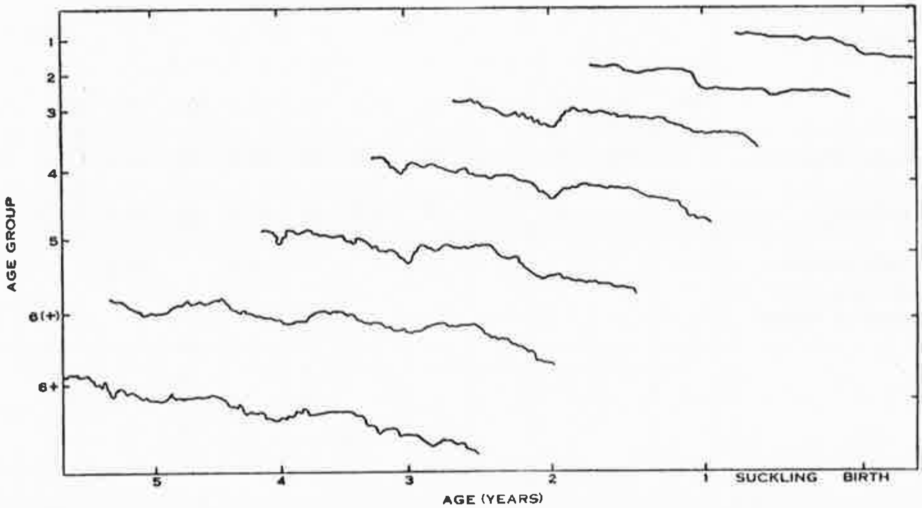

Fig. 1.—Examples of actual traces from baleen plates of humpback whales grouped according to age.

Wear at the tip of baleen plates makes age determination from baleen traces unreliable for individuals more than 6 years of age, so that although a few traces showed four or even five complete growth zones, all whales classified from the baleen as of 6 or more years of age were placed in the 6+ age group.

The example given of a 1-year old individual was taken from a small humpback whale killed under special licence. This female, 28 ft 9 in. long when killed on June 14, was in company with a lactating female and was still suckling, so was estimated to be approximately 10½ months of age.

The remaining age groups illustrated in Figure 1 have been spaced at yearly intervals in accordance with the evidence of Ruud and his co-workers that each growth zone in the baleen represents a span of 1 year.

(c) *Ear Plugs*

Ear plugs were stored in 10 per cent. formalin, then bisected longitudinally with a hand razor after orientating so that the cut surface exposed the widest face of the core of the plug. The face of each surface was then smoothed on a water stone. After cutting, the core of some plugs showed lines of fracture parallel to the laminations. In older (mature) individuals these "fracture lines" were generally regularly spaced, one between each dark band, but in younger (especially immature) whales fracture lines were often irregularly spaced, sometimes in groups, with little relationship to the laminations.

TABLE 1

FEMALE HUMPBACK WHALES: AGE (FROM BALEEN) AND OVARIAN CONDITION

State of Development	Baleen Age Group (Years)											
	1		2		3		4		5		6(+)	
	No.	(%)	No.	(%)	No.	(%)	No.	(%)	No.	(%)	No.	(%)
Sexually immature	4	100	8	87·5	22	88·0	23	63·9	33	42·3	14	5·9
At puberty			1	12·5	3	12·0	10	27·8	23	29·5	15	6·3
Sexually mature								8·3		28·2		87·9
Ovulations prior to season of killing												
1							1		14		38	
2							1		4		73	
3							1		2		45	
4									2		4	
5											4	
6											2	
7											4	
8											2	
9											5	
10											4	
11											4	
12											5	
13											3	
14											2	
15											4	
>15											11	
Total	4		9		25		36		78		239	

In most of the mature individuals the laminations in the core of the ear plug were clearly visible as a succession of dark bands which were narrower and more closely packed towards the base of the ear plug. In the course of this work it was noticed that while the laminations in mature males were almost always regularly spaced and of uniformly decreasing width (see Plate 1), the laminations in mature females frequently (but not always) showed irregularities in width, spacing, or pigmentation (see Plate 2). After a regular series of bands in the upper part of an ear plug, there may be a distinct but narrower, less pigmented lamination, followed by further bands of the earlier type. Sometimes a narrower lamination occurred again after two wider ones. It is suggested that increased nutritional demands in part of the female breeding cycle (pregnancy or lactation) may sometimes coincide with a poorer feeding season, the period of suboptimal nutrition being reflected in the ear plugs. From the available evidence it is suggested that this is more likely to occur in younger mature females (which are still growing) than in older females. Similar irregularities in the laminations were found in both ear plugs from the same individual.

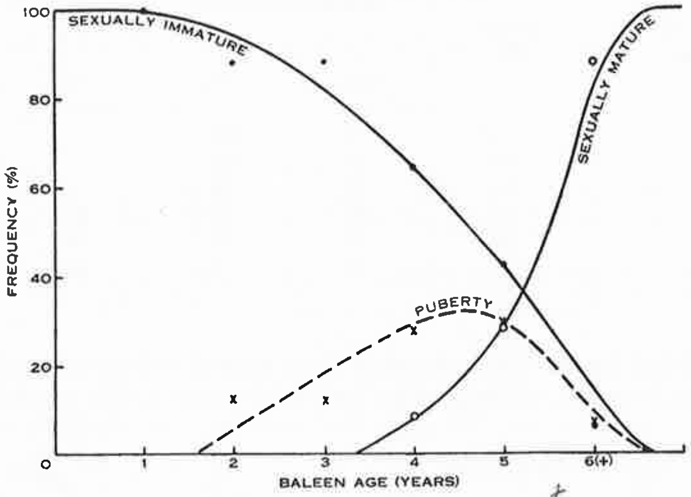

Fig. 2.—Age distribution of sexually immature, pubertal, and young mature female humpback whales as determined from baleen plates.

In some ear plugs (less than 10 per cent. of those examined) the laminations were partly or completely obscured by longitudinal striations giving a fibrous appearance to the core of the ear plug (Plate 3). In such cases the ear plugs have been rejected.

The laminations in younger (generally immature) whales were often poorly defined and lacking in pigment (Plate 4, Fig. 1). Sometimes the dark bands could be subdivided into two or three smaller bands placed close together (Plate 4, Fig. 2). In counting the laminations of these ear plugs only the wide, more regularly spaced bands have been used.

Attempts were made to dissect out the ear plugs from near-term foetuses, but only the secretory membranes were found.

IV. PUBERTY

(a) *Age at Puberty*

Since baleen traces obtained from samples collected on the west and east coasts of Australia gave similar ages at puberty, the data from the two areas are considered together in this regard.

Table 1 shows the ages (as determined from baleen) and ovarian condition of 391 female humpback whales. The proportions of sexually immature, puberal, and sexually mature females in each age group are plotted in Figure 2. The majority of females reach puberty at 4 or 5 years of age, while the upper limit of the age at puberty is close to 7 years.

TABLE 2

MALE HUMPBACK WHALES: AGE (FROM BALEEN) AND MATURITY, CLASSING MALES WITH TOTAL TESTES WEIGHT EXCEEDING 4 KG AS SEXUALLY MATURE

Baleen Age Group (Years)	Total No.	Sexually Immature		Sexually Mature	
		No.	(%)	No.	(%)
1	1	1	100		
2	14	14	100		
3	25	21	84·0	4	16·0
4	35	24	68·6	11	31·4
5	62	24	38·7	38	61·3
6(+)	101	10	9·9	91	90·1

Table 2 and Figure 3 show the ages (from baleen) and sexual condition in 238 male humpback whales, classing males with total testes weight exceeding 4 kg as sexually mature (Chittleborough 1955*a*). In males the mean age at puberty lies between 4 and 5 years; it is probable that slightly more males reach puberty at 5 years than at 4 years of age.

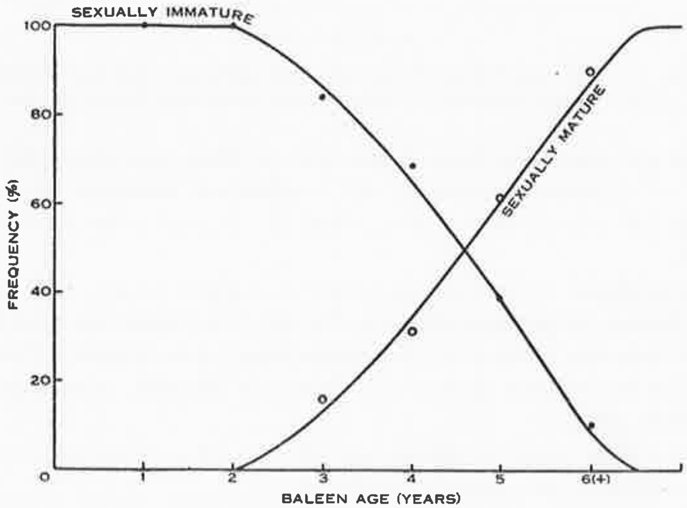

Fig. 3.—Age distribution of sexually immature and young mature male humpback whales as determined from baleen plates.

(*b*) *Ear Plugs at Puberty*

Table 3 shows the distribution of the numbers of ear plug laminations from 290 female humpback whales classified according to ovarian condition. This shows that at puberty the ear plugs may contain from five to 14 laminations with a mean of close to nine laminations.

Figure 4 shows the distribution of the numbers of ear plug laminations from 166 humpback whales grouped according to age (from baleen). In each year class the modal number of ear plug laminations lies at (or very close to) twice the number of years of age. Since most humpback whales reach puberty at 4 and 5 years of age, the mean number of laminations in the ear plugs at puberty is between eight and ten laminations.

TABLE 3

DISTRIBUTION OF NUMBERS OF EAR PLUG LAMINATIONS FROM 290 FEMALE HUMPBACK WHALES CLASSIFIED ACCORDING TO OVARIAN CONDITION

Number of Ear Plug Laminations	Numbers of Females		
	Sexually Immature	Puberal	Sexually Mature
4	1	—	—
5	3	2	—
6	6	3	—
7	7	2	2
8	6	—	5
9	2	4	4
10	4	2	11
11	1	2	12
12	—	1	16
13	—	—	17
14	1	—	17
15	—	—	7
16	—	—	14
>16	—	—	138

Much of the variation in the numbers of ear plug laminations within any one year class shown in Figure 4 may be attributed to poorly defined laminations often found in ear plugs of young whales (see Section III(*c*)).

V. RATE OF OVULATION IN MATURE FEMALES

The only direct method for determining the rate of ovulation in female whales is to mark calves or yearlings and examine the ovaries of the females when marked individuals are killed in later years. Little information of this type is available to date. One female humpback whale marked on the west coast of Australia when it was accompanied by a calf was killed and examined 9 years later. The ovaries then contained ten corpora albicantia, so that if this female had been marked at the end of its first pregnancy, the average rate of ovulation would have been 1·0 ovulation per year.

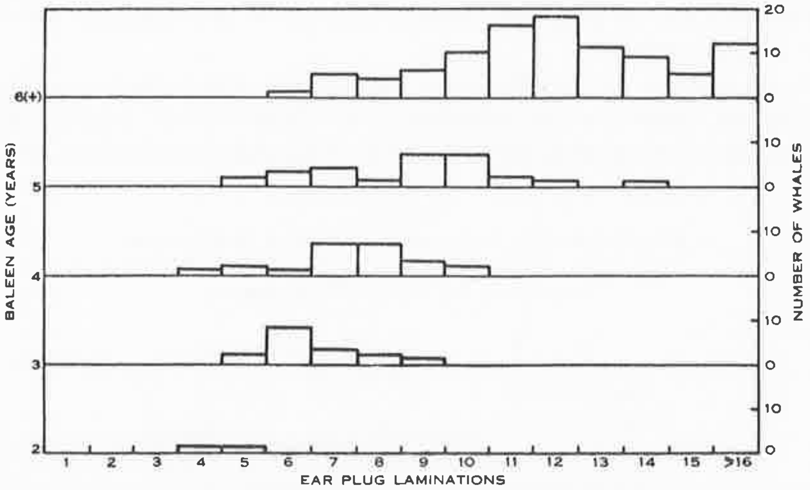

Fig. 4.—Relationship between age as determined from baleen plates and numbers of ear plug laminations in young humpback whales.

More precise information is available from another female which was also marked and later killed on the west coast of Australia. This female was accompanied by a small calf when marked in August 1954, so must have ovulated at least once in the winter of 1953. When killed in September 1956, the ovaries contained three corpora albicantia and one newly formed corpus luteum, while the ear plugs contained 14 laminations. Table 4 shows four variations in the possible sequence of ovulations in this female. It is probable that one of the first three variations actually occurred, in which case this female matured at 4 years of age (becoming pregnant) and had an average of one ovulation per year up to the time of killing.

Table 4

INFORMATION COLLECTED AND INFERRED FROM MARK A99, FIRED INTO A FEMALE WITH SMALL CALF ON AUGUST 17, 1954, RECOVERED ON SEPTEMBER 22, 1956

Possible Sequences of Ovulations	1952	1953	1954	1955	1956
Variation (*a*)	immature	2 ovulations	—	1 ovulation	1 ovulation
Variation (*b*)	immature	1 ovulation	—	2 ovulations	1 ovulation
Variation (*c*)	immature	1 ovulation	1 ovulation (post-partum)	1 ovulation	1 ovulation
Variation (*d*)	1 ovulation	1 ovulation	—	1 ovulation	1 ovulation
Number of ear plug laminations	6	8	10	12	14

TABLE 5

OVULATIONS OCCURRING IN 100 SEXUALLY MATURE FEMALE HUMPBACK WHALES DURING A 2-YEAR BREEDING CYCLE

(*A*) First Winter				(*B*) Second Winter		
Number of Females	Sexual Condition	Number of Ovulations		Number of Females	Sexual Condition	Number of Ovulations
5	No oestrous cycles	0	→	5	Oestrous cycles at same rate as in *A* (1·2 per female)	6
73	One oestrous cycle	73		5	Fail to conceive at *A* or lose early embryo so experience oestrous cycles as in *A*	6
19	Two oestrous cycles	38		5	Become pregnant in *A* but lose calf at birth so experience oestrous cycles as in *A*	6
3	Three oestrous cycles	9		10	Successfully give birth to calf conceived in *A*, then experience a post-partum ovulation (becoming pregnant while lactating)	10
				75	Successfully give birth to calf conceived in *A*, then may experience a post-partum ovulation, but this does not result in conception	0–75
100		120				28–103

In female humpback whales breeding cycles are of 2 years' duration and so extend over two winter periods when ovulation normally occurs (Chittleborough 1958*a*, Fig. 4). It is proposed here to estimate the total number of ovulations which occur in 100 females in the course of 2 years, considering the possible variations within the breeding cycle.

Ovulations occurring in sexually mature, non-pregnant females entering the first ovulatory period of a breeding cycle have already been studied (Chittleborough 1954). From this and further material it is estimated that in this period 100 mature females ovulate as given in part (*A*) of Table 5. The average number of ovulations per female in the first winter of a breeding cycle is then 1·2 ovulations.

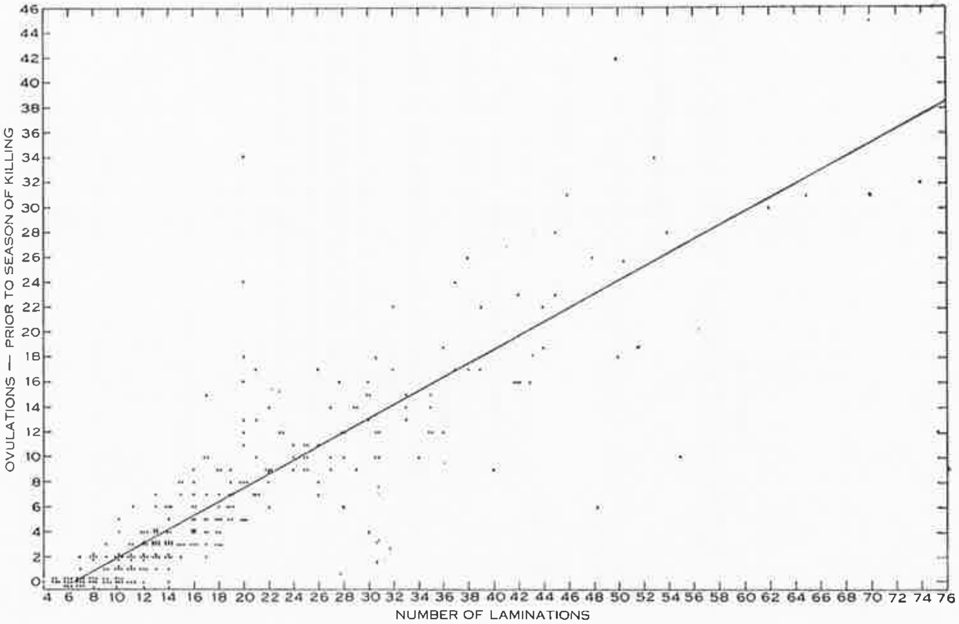

Fig. 5.—Relationship between numbers of previous ovulations and numbers of laminations in the ear plugs, for 287 female humpback whales.

Full details of ovarian activity in the second winter of the breeding cycle are difficult to obtain owing to the regulation prohibiting the killing of females accompanied by calves. The various conditions shown in part (*B*) of Table 5 have been found and described (Chittleborough 1958*a*), but the relative proportions given for each are largely speculative. Although post-partum ovulation does occur in the humpback whale (sometimes resulting in a female being simultaneously pregnant and lactating), it is not possible to determine by direct observation how often this occurs.

From the data given in Table 5, if post-partum ovulation is of infrequent occurrence, the total number of ovulations from 100 mature females in a 2-year breeding cycle is 148, while if post-partum ovulation is of regular occurrence the total number of ovulations is 223. Then the average rate of ovulation for mature female humpback whales lies between 0·74 and 1·12 ovulations per year.

VI. RELATION BETWEEN OVARIAN AND EAR PLUG DATA FROM FEMALES

In Figure 5 the number of ear plug laminations is plotted against the number of previous ovulations for each of 287 female humpback whales. The regression line calculated by the method of least squares is also shown. A few of the points lie very considerably above or below the regression line. This might be the result of unusually fast or slow rates of ovulation which may sometimes occur in individual

TABLE 6

DISTRIBUTION OF OVULATION COUNTS AND NUMBERS OF EAR PLUG LAMINATIONS, WITH CORRESPONDING SURVIVAL VALUES, FROM 158 SEXUALLY MATURE FEMALES

Ovaries				Ear Plugs			
Number of Previous Ovulations	Number of Females	Survivors		Number of Laminations	Number of Females	Survivors	
		No.	(%)			No.	(%)
		158	100			158	100
1	13	145	91·8	⩽10	18	140	88·6
2	28	117	74·1	12	23	117	74·1
3	16	101	63·9	14	23	94	59·5
4	15	86	54·4	16	13	81	51·3
5	8	78	49·4	18	14	67	42·4
6	9	69	43·7	20	15	52	32·9
7	8	61	38·6	22	8	44	27·8
8	7	54	34·2	24	5	39	24·7
9	10	44	27·8	26	8	31	19·6
10	8	36	22·8	28	6	25	15·8
11	2	34	21·5	30	6	19	12·0
12	6	28	17·7	32	3	16	10·1
13	4	24	15·2	34	2	14	8·9
14	4	20	12·7	36	1	13	8·2
15	3	17	10·8	38	1	12	7·6
16	5	12	7·6	40	1	11	7·0
17	4	8	5·1	42	3	8	5·1
18		8	5·1	44	3	5	3·2
19	1	7	4·4	46		5	3·2
20		7	4·4	48	1	4	2·5
21		7	4·4	50	1	3	1·9
22	2	5	3·2	52		3	1·9
23		5	3·2	54		3	1·9
24	1	4	2·5	56	2	1	0·6
25		4	2·5	58		1	0·6
26		4	2·5	>58	1		
27		4	2·5				
28		4	2·5				
29		4	2·5				
30	1	3	1·9				
>30	3						

females. It is also possible that one or two of the points well above the regression line might represent females whose ear plugs were of fibrous appearance (though not as fibrous as shown in Plate 3), so that laminations were partially obscured; this would result in much lower counts of laminations than were actually present.

The slope of the regression line ($y = 0{\cdot}558x - 3{\cdot}635$) gives the relationship of two ear plug laminations as equal to 1·12 ovulations. From this relationship it is possible to compare the mortality curves obtained from the same sample of mature females using the laminations in ear plugs and numbers of previous ovulations as independent methods of age determination. Table 6 shows the distribution of ovulation counts and numbers of ear plug laminations, with corresponding survival values, from 158 sexually mature female humpback whales sampled at random from the catch made at Carnarvon in 1957. The mortality curves derived from the two sets of data are shown in Figure 6, the scales on the abscissa axis being in the ratio of 2 ear plug laminations to 1·1 ovulations. The two curves are almost identical, showing good agreement between the two methods as applied.

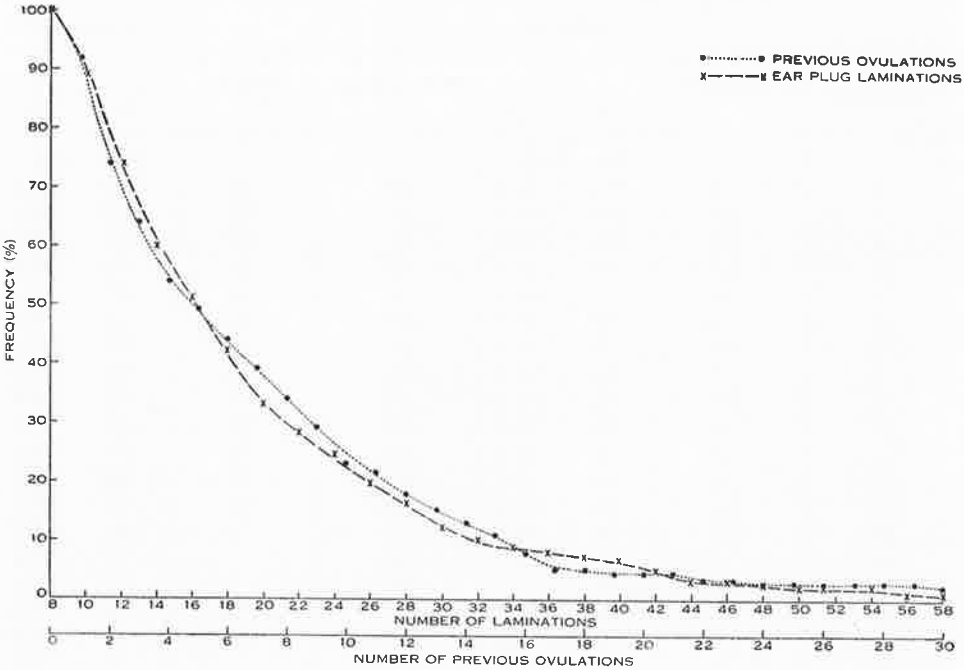

Fig. 6.—Mortality curves derived from the numbers of previous ovulations and from the numbers of ear plug laminations, for the same sample of 158 sexually mature female humpback whales.

VII. Comparison of Samples from Two Populations of Humpback Whales

Shore-based whaling stations on the west and east coasts of Australia operate upon separate populations of humpback whales known as Group IV and Group V respectively (see Mackintosh 1942). Using the methods described above it is possible to compare the age distribution within samples taken from these two populations.

TABLE 7

DISTRIBUTION OF NUMBERS OF EAR PLUG LAMINATIONS FROM SAMPLES OF TWO POPULATIONS

Number of Ear Plug Laminations	Mature Females				Mature Males			
	Carnarvon (Group IV)		Moreton Island (Group V)		Carnarvon (Group IV)		Moreton Island (Group V)	
	No. of Whales	(%)	No. of Whales	(%)	No. of Whales	(%)	No. of Whales	(%)
$\leqslant$10	18	11·4	2	2·7	53	33·1	13	7·9
12	23	14·6	3	4·1	22	13·8	17	10·3
14	23	14·6	9	12·3	22	13·8	9	5·5
16	13	8·2	7	9·6	14	8·8	12	7·3
18	14	8·9	8	11·0	11	6·9	9	5·5
20	15	9·5	6	8·2	7	4·4	11	6·7
22	8	5·1	4	5·5	6	3·8	11	6·7
24	5	3·2	1	1·4	1	0·6	8	4·8
26	8	5·1	3	4·1	4	2·5	10	6·1
28	6	3·8	2	2·7	4	2·5	6	3·6
30	6	3·8	2	2·7	2	1·3	8	4·8
32	3	1·9	3	4·1	2	1·3	6	3·6
34	2	1·3	2	2·7	1	0·6	4	2·4
36	1	0·6	4	5·5			6	3·6
38	1	0·6	3	4·1	1	0·6	2	1·2
40	1	0·6	1	1·4	2	1·3	3	1·8
42	3	1·9	2	2·7			2	1·2
44	3	1·9			1	0·6	4	2·4
46			3	4·1			3	1·8
48	1	0·6	1	1·4				
50	1	0·6	1	1·4	2	1·3	2	1·2
52					2	1·3	2	1·2
54			1	1·4			2	1·2
56	2	1·3					5	3·0
58								
60							2	1·2
62	1	0·6					1	0·6
64							1	0·6
66			1	1·4			1	0·6
70			2	2·7				
72							1	0·6
74			1	1·4			1	0·6
76			1	1·4	1	0·6	1	0·6
80					1	0·6		
84					1	0·6		
86							1	0·6
96							1	0·6
Total	158		73		160		165	

It is proposed here to consider only the sexually mature individuals. By doing so possible differences in gunner selection between the two areas would be minimized. Also by considering only mature whales the results are comparable with mortality curves calculated for samples of other species from Antarctic waters, using only pregnant females (see the reports to the International Whaling Commission for 1955 and 1958).

The samples compared were taken from Carnarvon (west coast) and Moreton Island (east coast) in 1957.

Table 7 shows the distribution of the numbers of ear plug laminations from the two samples. Figure 7 shows the percentage frequency distribution of the ear plug laminations for the females from the two samples, showing also the length frequency distribution and mean lengths of the same females. Although there is little difference between either the mean lengths or the length frequency distribution in the two samples, the distribution of ages (from the ear plugs) is quite different, there being more young females and less of the older individuals in the sample of females from the west coast than in that from the east coast of Australia.

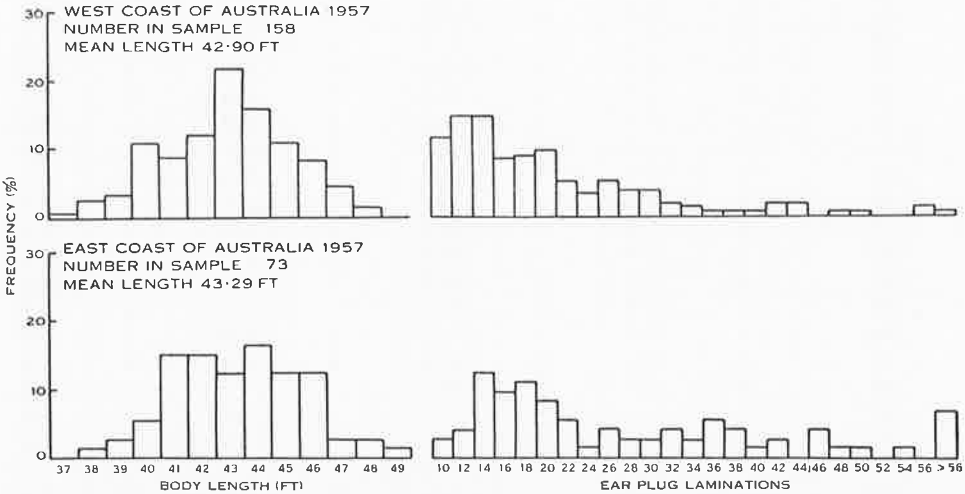

Fig. 7.—Mean lengths, length frequency distributions, and distribution of ages (from ear plug laminations) for samples of sexually mature females from the west and east coasts of Australia in 1957.

Figure 8 shows the corresponding information for the males sampled in the two areas. In this case there is some difference in the mean lengths, considerable difference in the length frequency distribution, and a great difference in the distribution of ages (from the ear plugs), the sample from the west coast containing far more young mature males.

Figure 9 shows mortality curves constructed from the data in Table 7. The variations in the curve representing the females sampled on the east coast of Australia are probably the result of the smaller sample, but the curve generally follows that of the males sampled in the same locality. The mortality curve derived for the mature males examined on the west coast is steeper than that of the corresponding sample of females, and both are much steeper than the mortality curves of either males or females from the east coast of Australia.

VIII. Discussion

Seasonal variations in the thickness of the cortical layers of the baleen afford a useful method of age determination in both sexes for the first 5 years of life (up to puberty) but wear at the tip of baleen plates prevents their use for determining the age of older (mature) individuals. Baleen traces from the younger individuals have proved most useful in establishing the rate of accumulation of laminations within the core of ear plugs.

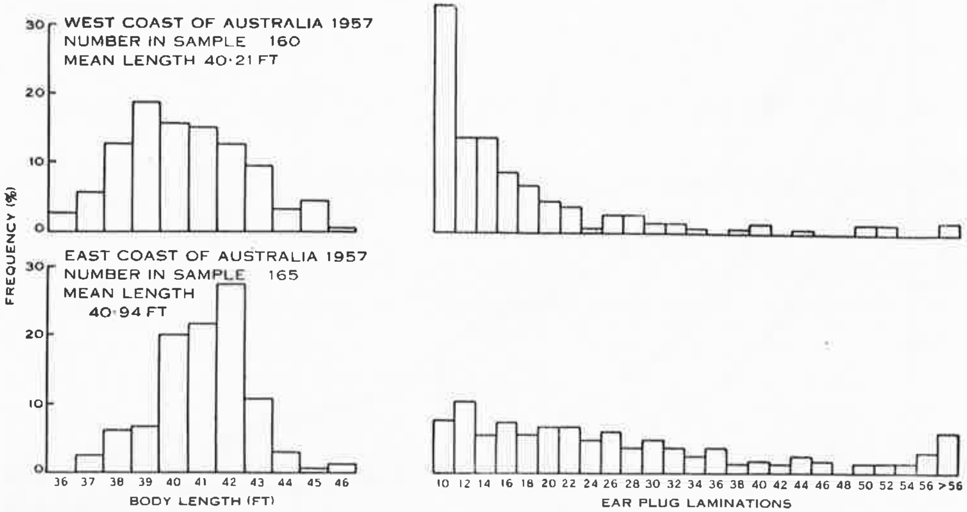

Fig. 8.—Mean lengths, length frequency distributions, and distribution of ages (from ear plug laminations) for samples of sexually mature males from the west and east coasts of Australia in 1957.

From the examination of the auditory meatus of near-term foetuses it would appear that the first lamination of the ear plug is laid down soon after birth. Thereafter two laminations are formed each year. At puberty a mean of nine laminations are present.

It has been pointed out that the laminations within the ear plugs of young (immature) whales are often poorly defined and lacking in pigment. As these earlier laminations become compressed at the top of the ear plug core during later years of life they may become more difficult to distinguish so that counts of the laminations in the ear plugs of mature individuals may be slightly below the actual number laid down. For this reason the ages of mature whales as determined from the ear plugs should be regarded as minimum ages. However, assuming the possible error to be slight and relatively constant, the ear plugs afford the best method available at present for age determination in the Mysticeti.

The regression line representing the relationship between numbers of ear plug laminations and numbers of previous ovulations (Fig. 5) passes through the abscissa axis at 6·5 ear plug laminations instead of between 8 and 10 laminations as shown by other methods. This is the result of the tendency for the counts of laminations within the ear plugs of mature individuals to be slightly below the actual number present. Most of the data used in the calculation of this regression line were obtained from mature females.

Since the possible error in counts of ear plug laminations is considered to be fairly constant in the mature females, the slope of this regression line is close to the true relationship, so that after attainment of puberty two ear plug laminations are equivalent to an average of 1·1 ovulations. This is circumstantial evidence in support of the theory that post-partum ovulation is of common occurrence (although perhaps not often successful) in the female humpback whale, as it has been shown from the examination of ovaries (Section V) that if post-partum ovulation is of regular occurrence the mean rate of ovulation would be 1·12 ovulations per year.

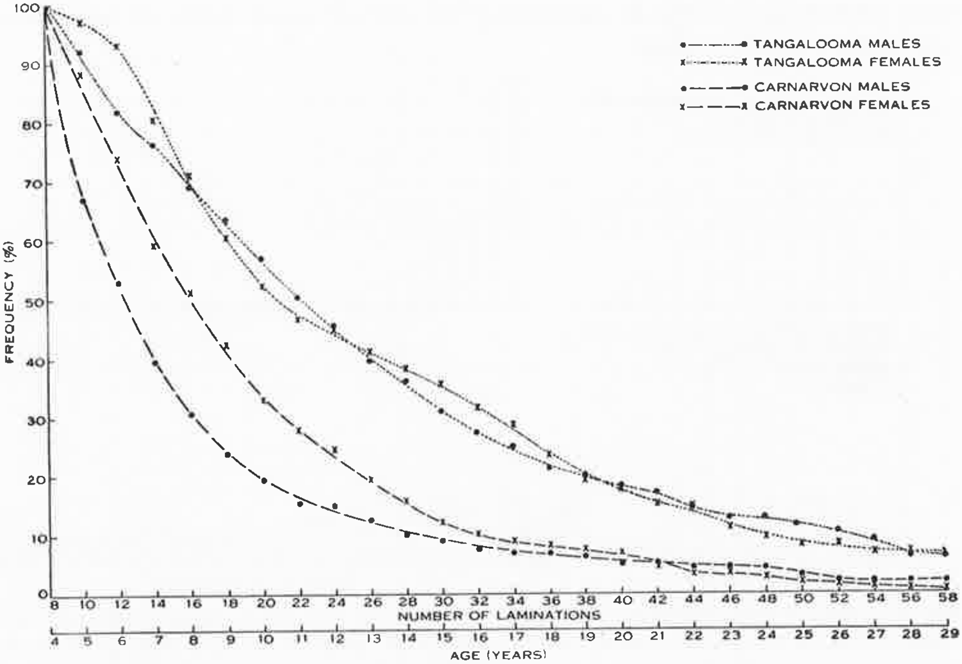

Fig. 9.—Mortality curves for mature male and female humpback whales sampled in 1957 on the east coast at Tangalooma and on the west coast at Carnarvon.

The regression line representing the relationship between numbers of ear plug laminations and numbers of previous ovulations ($y = 0\cdot558x - 3\cdot635$) is similar to that obtained by Symons and Weston (1958) for approximately 30 female humpback whales taken in Antarctic waters ($y = 0\cdot59x - 3\cdot4$). In this case two ear plug laminations would be equivalent to 1·18 ovulations.

Since the mortality curves derived separately for the same females using ear plug laminations and numbers of previous ovulations are the same when plotted on the scale ear plug laminations : previous ovulations = 2 : 1·1, the two methods may replace each other in samples of mature females where complete data were obtained from only one of these organs.

When determining the age of a single whale by the three methods studied in this paper, the method using baleen plates is considered to be the most accurate for a whale of up to 5 years of age, while for an older female the number of laminations within the ear plugs gives a much more reliable index of age than the number of previous ovulations. Figure 5 shows that if the rate of accumulation of ear plug laminations is constant throughout life, then the rate of ovulation may vary considerably from one female to another. The rate of ovulation may also vary between puberty and old age within each individual. For these reasons the age of a mature female as estimated from the number of previous ovulations (using an average of 1·1 ovulations per year, and a mean age of 4 or 5 years at puberty) gives only a "mean age" of that female. Although this may be less accurate than the age as determined from ear plug laminations, the method using numbers of previous ovulations gives a useful index of the age distribution within a large sample of mature females.

In the comparison of age distribution and mortality curves obtained from collections of ear plugs from sexually mature individuals from the west and east coasts of Australia in 1957, it has been shown that the sample from the west coast contained a far higher proportion of young individuals than present in the sample collected on the east coast.

This difference cannot be attributed to differences in the times of passage of various age groups past the sampling points in the two localities, as the samples were collected in similar latitudes and throughout the northward migration of the humpback whales on the west and east coast of Australia.

Assuming that the samples were representative of the mature individuals in the populations passing along these coasts in that year, the evidence from age distribution and mortality curves strengthens the previous evidence (Chittleborough 1958*b*) of a decline in the Group IV stock of humpback whales. Further, the steeper mortality curve for males than for females sampled on the west coast indicates that the mature males in that stock have been affected more than the mature females. The explanation of this is based on the fact that males reach puberty at considerably shorter lengths than females. In earlier years (from 1949) the intense catching from the Group IV stock has been concentrated upon mature individuals in the case of the males, but spread over a wider range of age groups, including more immature individuals, in the case of the females. As a result of this, by 1957 fewer older males than females remained in this population.

When comparing the age distribution in the samples from the two stocks it might be argued that more careful selection on the east coast resulted in more of the older individuals being taken in this area than in the catch made on the west coast. As stressed earlier, in the comparison of samples from the two areas (Section VII) only mature individuals have been used. This minimizes possible differences in the degree of selection because after sexual maturity has been attained the rate of growth is less and decreases fairly rapidly in succeeding years.

Although it is not possible to measure and compare the "selection factor" as applied by individual gunners or by gunners in different localities, it is considered that the evidence based upon age distribution as determined from ear plugs shows that at present there are real differences in the age distribution of the two populations of humpback whales which migrate along the west and east coasts of Australia respectively.

It is well known from population studies upon other animals that commercial operations (or other sampling by man) upon an accumulated population initially cause a reduction in the proportion of old individuals in that population, which may then stabilize at a lower mean age (Nicholson 1954). However, from the comparison of the age distribution (over several years) in samples of humpback whales from the west and east coasts of Australia it would appear that the population migrating along the west coast has not stabilized during several years of commercial catching, but is continuing to decline.

IX. Acknowledgments

The cooperation of the Norwest Whaling Company, Cheynes Beach Whaling Company, and Whale Products Pty. Ltd., enabling material to be collected from their respective stations at Carnarvon, Albany, and Moreton Island is acknowledged.

Commonwealth and State Fisheries Inspectors gave valuable assistance in the collection and sorting of material.

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Fig. 1.—Ear plug from a mature male humpback whale: 95 regular laminations (very crowded at the base).

Fig. 2.—Ear plugs from a mature male humpback whale: 36 regular laminations.

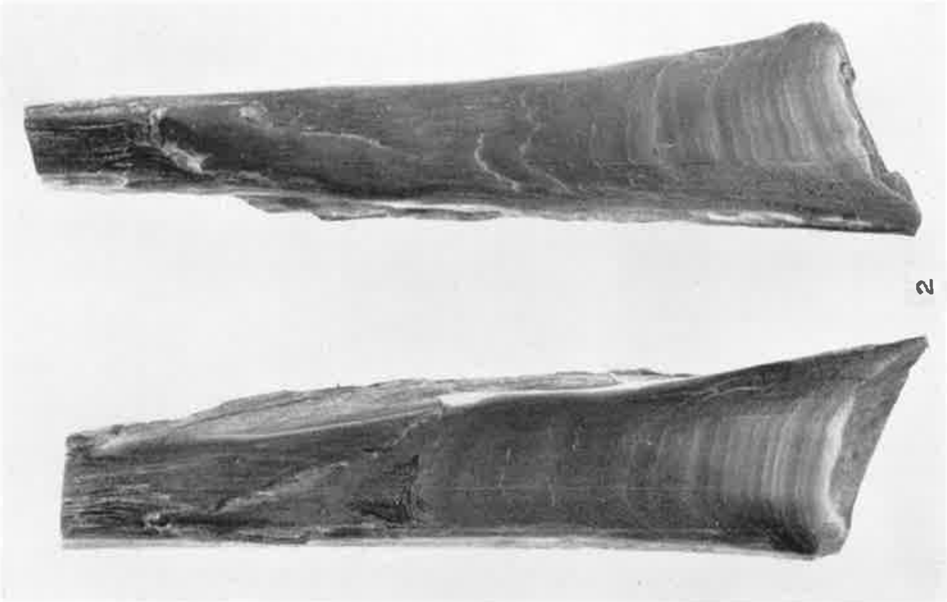

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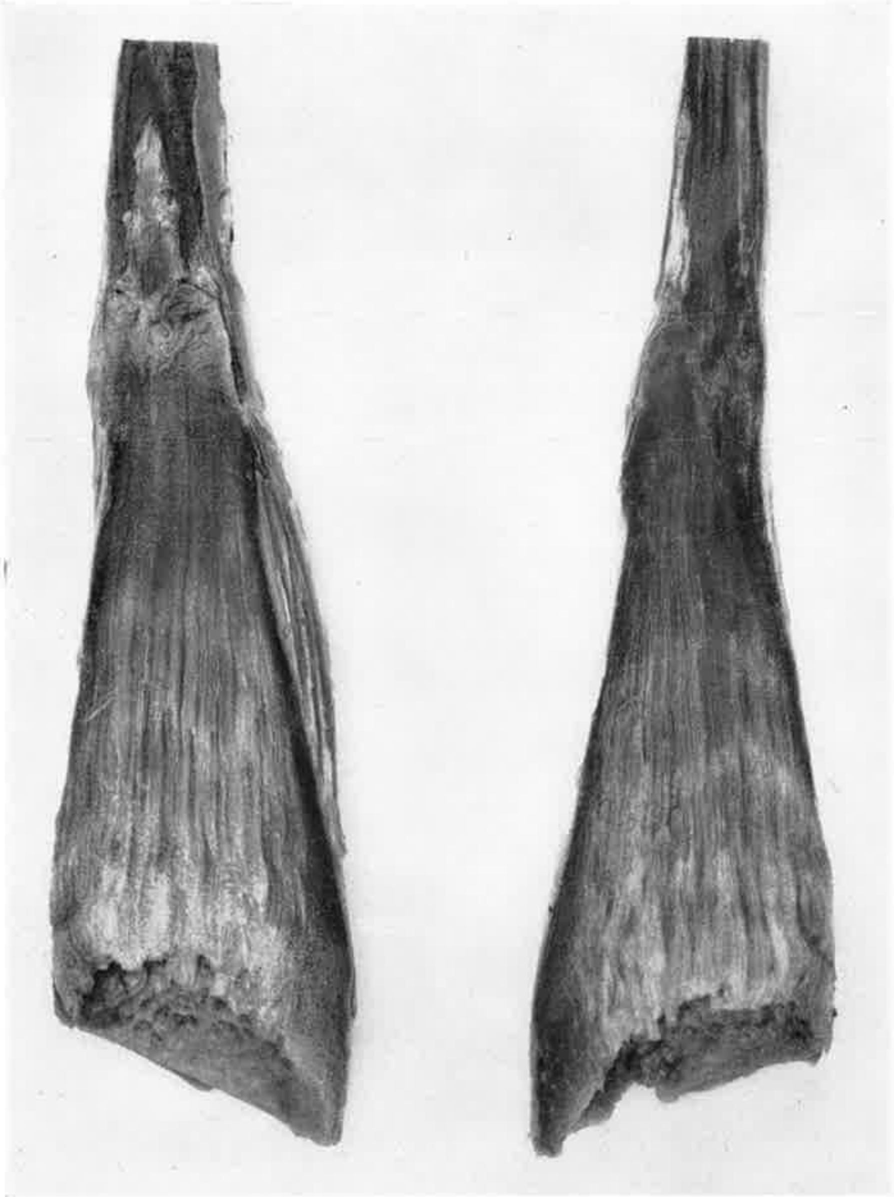
Fig. 1.—Left and right ear plugs from a mature female: 22 laminations, some irregularities in width and pigmentation. Eight corpora albicantia recorded from the ovaries.

Fig. 2.—Left and right ear plugs from a mature female: 22 laminations, lower ones irregular in width. Six corpora albicantia recorded from the ovaries.

DETERMINATION OF AGE IN HUMPBACK WHALES



Ear plugs of fibrous appearance, rejected as no reliable count of laminations was possible.

DETERMINATION OF AGE IN HUMPBACK WHALES

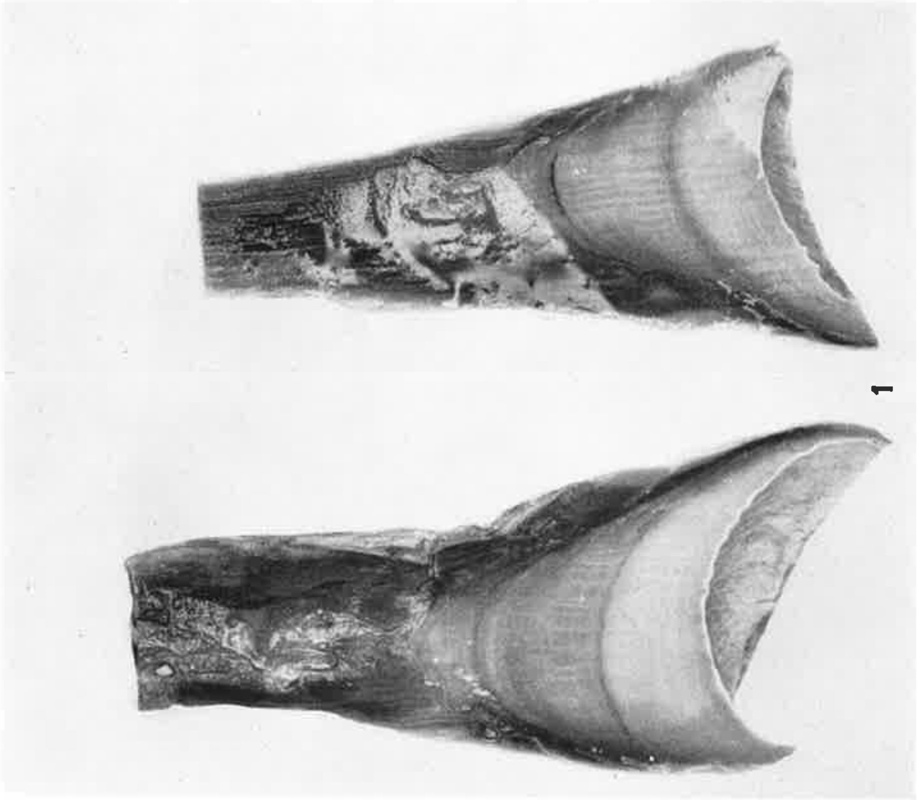


Fig. 1.—Ear plugs from an immature male (length 33 ft 5 in.). Approximately five pale, poorly defined laminations.

Fig. 2.—Ear plug from a young (recently matured) male: 11 laminations, most broken by lines of fracture.

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Paper 10

COMMONWEALTH OF AUSTRALIA
COMMONWEALTH SCIENTIFIC AND INDUSTRIAL
RESEARCH ORGANIZATION

(*Reprinted from Nature, Vol.* 187, *No.* 4732, *p.* 164 *only,*
July 9, 1960)

Marked Humpback Whale of Known Age

THE determination of age in humpback whales has been by indirect methods using baleen plates and ear plugs. By these methods, I found that humpback whales in Australian waters reach puberty between 3 and 7 years of age, the majority of puberal whales being 4 or 5 years[1]. Nishiwaki[2], using the ear plugs from humpback whales taken in North Pacific waters, found that the average age at sexual maturity was 5 years.

Until recently it has not been possible to check these results by direct evidence from marked whales. Dawbin[3] obtained some evidence from two humpback whales marked in New Zealand waters when at least 1 year old and recaptured after 12 and 19 months respectively. Since both were sexually immature when killed, Dawbin showed that the minimum age at sexual maturity was 3–4 years. Ear plugs and baleen plates were collected from one of these whales, and the present methods of interpretation of these organs for age determination gave results consistent with the probable age of this individual.

Further information is now available from a humpback whale marked (Mark No. 11689) on October 6, 1954, at 27° S. 153½° E., when it was migrating southwards on the east coast of Australia. It was then recorded as a yearling approximately 30 ft. in length. This mark was recovered on August 26, 1959, from a male humpback shot at 25° 21′ S. 112° 26′ E. off the west coast of Australia.

As ear plugs, baleen plates, and testis weights were obtained from this specimen, it has been possible to compare the age estimated from these organs with the known minimum age. Following the method of interpretation of baleen traces described by me[1], the age of this whale was determined as at least 5 years. The ear plugs contained 12 laminations, and, using the postulate of two laminations per year, the age of this whale was estimated at 6 years. Since the whale was at least at the beginning of its second year when marked, it was probably 6 years of age when shot.

So the indirect methods using baleen plate traces and ear plug laminations give estimates of age in good agreement with the known age.

The testes each weighed 1·0 kgm., which indicates[5] that this whale was sexually immature, and that puberty would probably have been attained at 7 years of age. This is above the age at which most male humpbacks have been estimated to reach puberty; but it is not an isolated example since, of 118 males (from the west coast of Australia) the ear plugs of which contained 12 laminations, 6 per cent were still sexually immature.

The body-length of this whale was recorded as 36 ft. 9 in., which is relatively short for a male of 6 years but within the range of lengths recorded for males of that age. In 164 males from Australian whaling stations estimated on the evidence from ear plugs to be 6 years old, the body-lengths ranged from 34 ft. 7 in. to 43 ft. 3 in. with a mean length of 39·11 ft., standard deviation 1·62 ft., and a standard error of mean 0·13 ft. It is therefore probable that this was a slow-growing individual relatively late in maturing.

The recovery of this mark is also of interest because it is the first recovery on the west coast of a mark fired into a whale on the east coast of Australia. This change of migration path followed the mingling during the summer of 1958–59 of some of the group V (130° E.–170° W.) with the group IV (70° E.–130° E.) dopulation of humpback whales which I[4] have shown in the region of the Antarctic from 110° E. to 130° E.

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Division of Fisheries and Oceanography,
Commonwealth Scientific and Industrial
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Sydney, Australia.
Jan. 14.

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Paper 11

Commonwealth of Australia.
COMMONWEALTH SCIENTIFIC AND
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An Analysis of Recent Catches of Humpback Whales from the Stocks in Groups IV and V

Prepared for
the International Whaling Commission
By
R. G. Chittleborough

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SUMMARY

Recent catches (from 1949/50 to 1955/56) of humpback whales from the southern stocks known as Groups IV and V are analysed.

The composition of catches from the Group IV stock (Western Australia and Antarctic region between longitude 70° E. to 130° E.) progressively declined from 1949 to 1954. Following a reduction in the quotas allotted on the Western Australian coast, the composition of the 1955 and 1956 catches in this region improved very considerably. This was largely due to the more stringent selection of larger whales in those years. The catch of humpback whales from Antarctic Area IV in 1956 showed slight improvement in some (but not all) aspects.

In the Group V stock, (longitude 130° E. to 160° W.), the composition of catches on the eastern Australian coast was reasonably stable from 1952 to 1953, but showed some less favourable trends in 1954. The improved composition of catches on the eastern Australian coast in 1955 and 1956, following immediately upon the reduction of Western Australian quotas, might indicate that the cut in the west stimulated more careful selection on the east coast.

In contrast, the composition of catches in Antarctic Area V declined in 1955 and 1956. Assuming the selection factor had remained at about the same level, this suggests a slight decline in the condition of the Group V stock.

The analyses of the material available from recent catches in the Groups IV and V stocks of humpback whales suggest that the stocks will not withstand continuous fishing above the present (1956) intensity.

In a comparison of humpback whaling in Antarctic and temperate waters, it appears that better utilization and management of these stocks is at present possible in temperate rather than Antarctic waters.

I. INTRODUCTION

The Group IV stock of humpback whales is that fished in Antarctic waters between longitudes 70° E. and 130° E. during the southern summer, and on the Western Australian coast in the winter.

In the Antarctic the open season for the taking of humpback whales is confined to the first four days of February in each year. This has been done in order to restrict the total catch of humpback whales from Antarctic waters to approximately 1250 per year. In the 1956 season a total of 1432 humpback whales was taken in this four day season in the Antarctic.

On the Western Australian coast, the three stations which operated up to 1955 (at Point Cloates, Carnarvon, and Albany) were allotted separate annual quotas. Until 1954, the annual quotas were as follows — 1951, 1250; 1952, 1250; 1953, 1300;

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*) An Officer of the Division of Fisheries and Oceanography, C.S.I.R.O., Cronulla, Sydney.

1954, 1320. Prior to the 1955 season the quotas at the two larger stations (at Point Cloates and Carnarvon) were reduced by 100 humpbacks each, so that the total catch allowed on the Western Australian coast in 1955 and 1956 was 1120 humpback whales. This reduction was made because of evidence of some deterioration in the Group IV stock.

In 1956 the station at Carnarvon, previously operated by the Australian Whaling Commission, was sold to the Nor' West Whaling Company. This company did not operate its station at Point Cloates (22°35' S, 133° E.) during the 1956 season, but combined the quotas of the two stations (each of 500 humpback whales) and concentrated catching vessels and equipment at Carnarvon.

The Group V stock of humpback whales is that fished in Antarctic waters between longitudes 130° E. and 160° W. during the southern summer, and on the coasts of New Zealand, eastern Australia, and Norfolk Island in the winter.

The two whaling stations on the eastern coast of Australia (at Tangalooma and Byron Bay) have been allotted annual quotas of 600 and 120 humpback whales respectively. The small whaling station on Norfolk Island, some 800 miles east of Australia, was opened in 1956. A quota of 150 humpback whales was granted to this station for its first season, and in subsequent seasons 120 humpbacks or such other number as the Minister may determine in the light of scientific evidence regarding the stocks of whales and the need for the conservation of resources.

The five whaling stations operated by Australia filled their quotas in the 1956 season. The individual catches at each station were: —

Western Coast

Carnarvon (24°53' S, 113°38' E.) Nor' West Whaling Company Ltd. 1000 humpback whales.

Albany (35°05' S, 117°56' E.) Cheynes Beach Whaling Co. Pty. 119 humpback whales, 1 fin whale.

Eastern Coast

Tangalooma (27°11½' S, 153°23½' E.) Whale Products Pty. Limited 600 humpback whales.

Byron Bay (28°37½' S, 153°38' E.) Norfolk Is. and Byron Bay Whaling Co. Ltd. 120 humpback whales.

East of Australia

Norfolk Island (25° S, 167°58' E.) Norfolk Is. and Byron Bay Whaling Co. Ltd. 150 humpback whales.

The analysis of the catch returns of these whaling stations (as well as those of the station at Point Cloates) up to the end of the 1956 season, are pre-

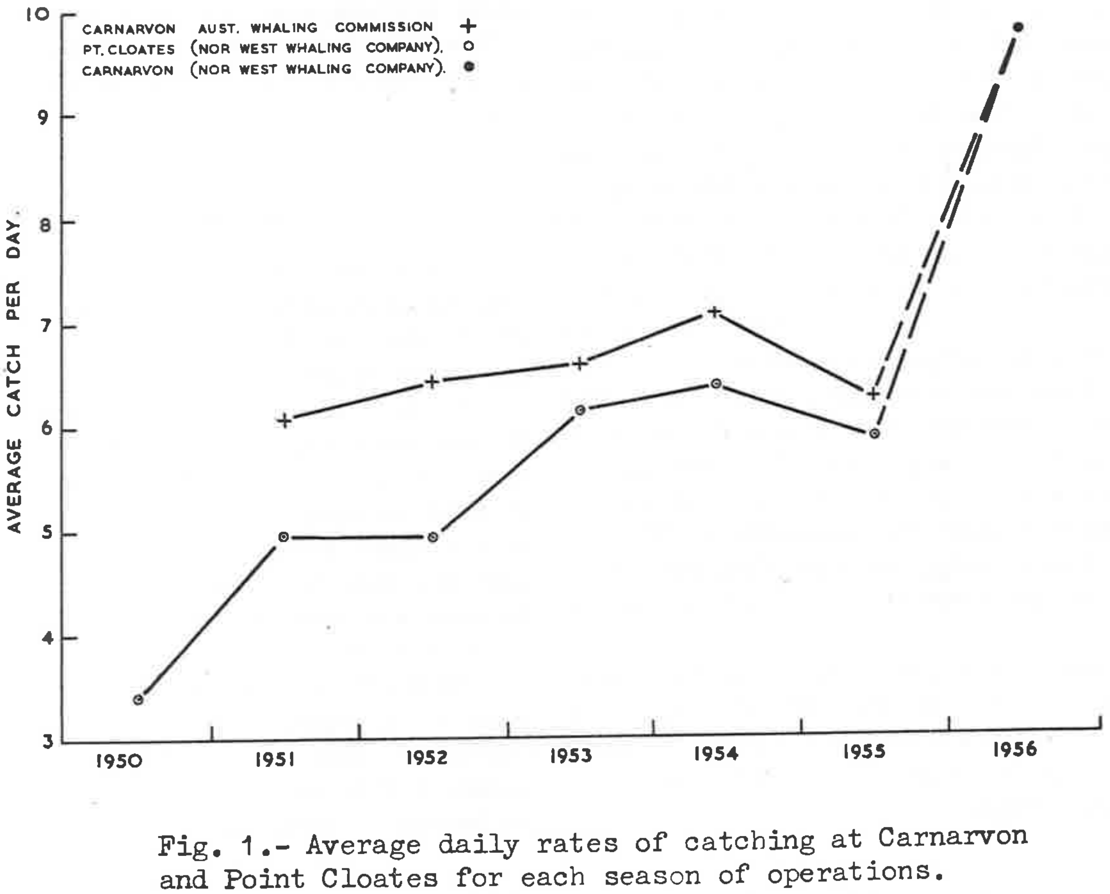


Fig. 1.- Average daily rates of catching at Carnarvon and Point Cloates for each season of operations.

sented in this report. Catches of humpback whales from Areas IV and V of the Antarctic from 1950 to 1956 are also analysed, so that the effects of the total fishing effort upon the two populations may be examined.

II. GROUP IV

(a) General.

The closing of the station at Point Cloates and the transfer of its humpback quota, catching vessels, and certain machinery to the Station at Carnarvon, has meant that in the 1956 season there has been some change in the fishing effort on the Western Australian coast. This must be considered when studying the results of that season.

The increased capacity of the Carnarvon factory enabled that station to process a greater number of whales per day (Fig. 1) in 1956 than in previous years. Whilst the average number of whales taken per day increased over previous years the average rate per catcher day compares with the 1955 figure for the Point Cloates Station. This is demonstrated in Table 1 where the average catch per catcher day at Carnarvon and Point Cloates is shown for each season from 1950.

The gunners of the catchers operating from Carnarvon in 1956 were required as in 1955 to select carefully the largest whales available. The greater concentration of catching power might be expected to allow the selection of larger whales to be applied more effectively.

(b) Sex Ratio.

Table 2 shows the numbers and percentages of females in the seasonal catches of humpback whales for individual coast stations, the combined catches of Western Australian coast stations, and for Antarctic Area IV, from 1949 to 1956.

In a comparison between the two areas, it is seen that in earlier seasons (1949—1951), females dominated catches in Antarctic Area IV, while males were predominant in catches from the warmer waters of the Western Australian coast. This has been accepted as the normal condition found in stocks of humpback whales which have not been over exploited.

In more recent years (1952—1955), the proportion of females in the catches declined in Antarctic Area IV, and rose on the Western Australian coast, so that in both areas the catches contained almost the same numbers of males and females. Whatever the reason for the marked disparity normally found between the sex ratios in catches from Antarctic and temperate waters, its disappearance in recent years within the Group IV stock suggests that this population has been adversely affected.

In 1956 the proportion of females in the catch has increased in Antarctic Area IV and decreased in the total catch on the Western Australian coast.

The rise in the percentage of females in the 1956 catch from Antarctic Area IV is difficult to interpret on the information available. It might be suggested that it resulted from a more careful selection of larger individuals, but this is not confirmed by an examination of the catch.

The fall in the percentage of females taken on the Western Australian coast during 1956 is simply due to the change in the catching conditions in that year. In 1956 the quota previously taken at Point Cloates was transferred to Carnarvon (where the proportion of females has always been lower than in catches at Point Cloates, as shown in Table 2). At Carnarvon 1000 humpback whales were taken in 1956 compared with 500 humpbacks in 1955. This extended the catching period in 1956 for four weeks

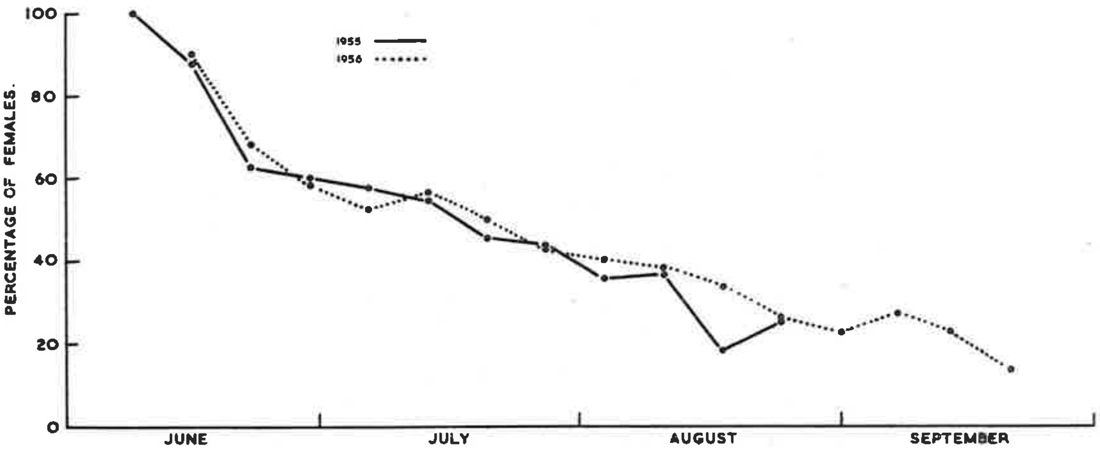


Fig. 2.- Percentages of females in the catches during each week of operation at Carnarvon in 1955 and 1956.

longer than in 1955, and in this month (September) the proportion of females in that region is always low. This is evident in Figure 2 which shows the percentages of females in weekly catches at Carnarvon during 1955 and 1956. Over the same period of operations in these years, the proportions of females were almost identical.

(c) Mean Lengths.

Table 3 lists the mean lengths of males and females for the annual catches of individual and combined stations on the Western Australian coast, as well as those for Antarctic Area IV from the 1949/50 season to that of 1955/56.

At Carnarvon, the mean lengths of both males and females were almost the same in 1956 as in 1955, considerably higher than in previous seasons. When the catches for all Western Australian coastal stations are combined, the mean lengths of both males and females were higher in 1956 than in 1955. This is mainly due to the fact that in the 1955 season when the Point Cloates station was operating, the mean lengths of both the males and females at that station were lower than at Carnarvon, tending to depress the mean lengths of the combined catch in that season.

Figure 3 shows the mean lengths of all males and females taken each year from 1949 on the Western Australian coast and from Antarctic Area IV. The total catches of humpback whales from this Group IV stock (Antarctic Area IV plus Western Australian coast) for each year from 1949 to 1956 are also set out in Figure 3. This figure shows that

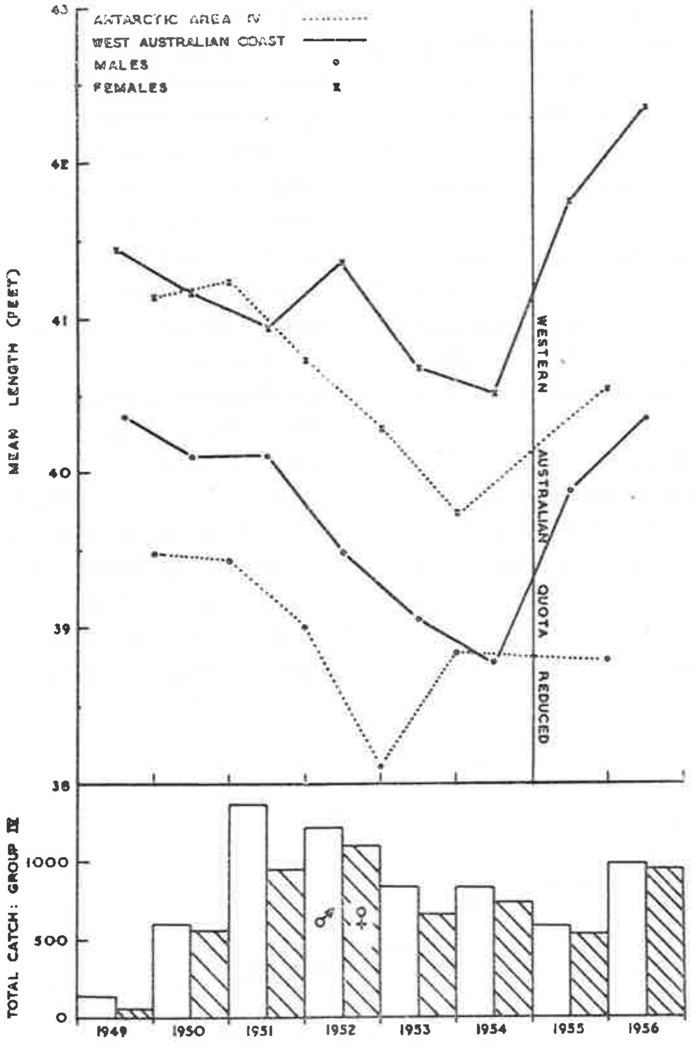


Fig. 3.- Above: Mean lengths of males and females in seasonal catches of combined Western Australian shore-stations and of Antarctic Area IV.
Below: Total catches of males and females from the Group IV stock in each year from 1949 to 1956.

with a total catch exceeding 2,000 humpback whales both in 1951 and 1952 and only slightly lower catches in succeeding years, the mean lengths of males and females taken both on the Western Australian coast and in the Antarctic, declined from 1951 until 1954. As far as is known, the degree of selection of whales for killing was approximately constant over these years.

On the Western Australian coast, since the reduction of the quotas (prior to the 1955 season), the mean lengths of both males and females have returned to the levels of earlier years; in fact the mean length of the females is now considerably higher than ever before. In contrast the mean lengths of males and females taken in Antarctic Area IV during 1956, while showing some increase in the case of the females, remained well below the means for earlier seasons (1949/50 and 1950/51). This emphasises that in the last two seasons there has generally been far more stringent selection of the larger humpback whales on the Western Australian coast.

(d) Length Frequencies.

The length frequency distribution of the male humpback whales taken each year by combined stations on the Western Australian coast and also for corresponding seasons in Antarctic Area IV is shown in Table 4. From this table it can be seen that up to 1954 there has been a marked swing towards the lower length ranges in the catches both from the Western Australian coast and also from Antarctic Area IV.

In the catches of males on the Western Australian coast during 1955 and 1956, the length frequency distribution improved considerably, returning in 1956 to a similar distribution as in 1951. On the other hand, the length frequency distribution of males taken in Antarctic Area IV in 1956 showed little improvement upon that of the 1954 catch in Antarctic Area IV.

Table 5 shows the length frequency distribution of the females in the same seasons and regions as for the males in Table 4. In the case of the females (Table 5) there has also been a swing, up to 1954, towards the lower length ranges. However, with the females, although the numbers in the lower length groups increased, the drop in the higher length groups was less marked than in the males.

In 1955 and 1956, the length frequency distribution of the females taken on the Western Australian coast improved greatly, in fact in 1956 it was better than in any previous year. However, although there was some improvement in the length

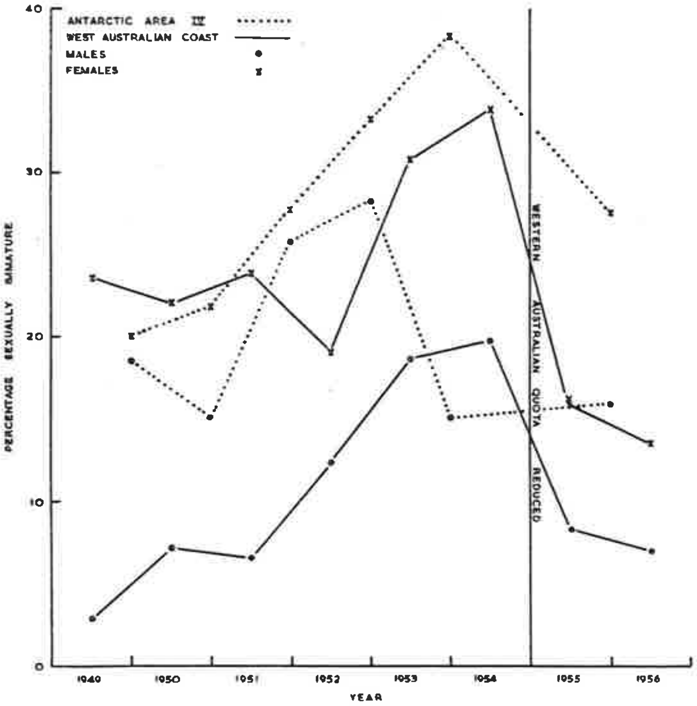


Fig. 4.- Percentages of sexually immature males and females in yearly catches of combined Western Australian stations and of Antarctic Area IV.

frequency distribution of females taken in Antarctic Area IV during 1956, the distribution remained lower than that in 1950 and 1951 catches in the same region.

(e) Sexually Immature Whales.

It has been demonstrated that on the Western Australian coast male humpback whales reach puberty at a mean length of 36 feet 9 inches (Chittleborough 1955*a*) and the females reach puberty at a mean length of 38 feet 6 inches (Chittleborough 1955*b*). In this report it is proposed for convenience to consider those males at or less than 36 feet 6 inches and females at or less than 38 feet 6 inches in length as sexually immature individuals. On this basis the percentages of immature males and females within a commercial catch may be calculated with reasonable accuracy.

Table 6 lists the numbers and percentages of immature males and females in the catches of individual and combined stations on the Western Australian coast, and in the catches from Antarctic Area IV, for each season of operation from 1949 to 1956. Figure 4 shows the percentages of immature males and females in the yearly catches of each sex from the Western Australian coast and from Antarctic Area IV.

In the case of males, the proportion of immature individuals in the Western Australian catch (Fig. 4) increased from 1949 to a maximum in 1954. After 1954 the quotas at the two larger stations were reduced and in 1955 and 1956 the percentage of immature males in the Western Australian catch decreased very considerably. In Antarctic Area IV, the percentage of immature males, generally higher than in the Western Australian catches, rose to a high peak in 1953, fell in 1954, and in 1956 remained at a similar level to that in the 1954 catch.

In the case of the females, Figure 4 shows that from 1949 to 1954 the proportion of immature individuals in the catches of females rose very considerably both on the Western Australian coast and also in Antarctic Area IV. However, on the Western Australian coast, following the reduction in the humpback quota, the percentage of immature females decreased sharply in 1955 to a lower level than in any previous years. In 1956 the proportion

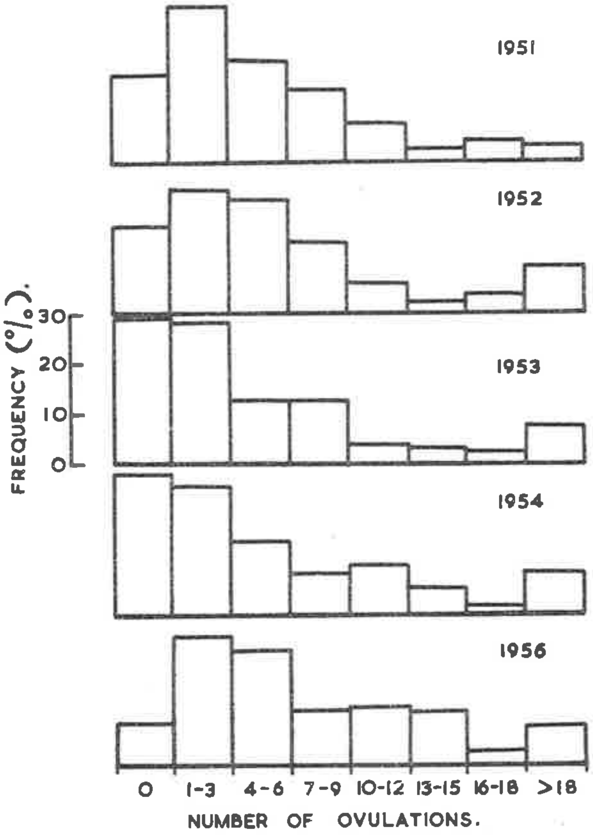


Fig. 5.- Relative age distribution (based on ovulation counts) of females sampled from catches on the Western Australian coast.

of immature individuals in the catch of females from the Western Australian coast decreased even further. This was mainly the result of the closing of the station at Point Cloates and the concentration of catching effort at Carnarvon. In Antarctic Area IV, the percentage of immature females was lower in 1956 than in 1954, but was still well above the level of earlier seasons and almost three times that of the 1956 catch on the Western Australian coast.

(f) Ovulation counts as an index of the relative age distribution in catches of females.

It is known that corpora albicantia persist in the ovaries of whales for very long periods, if not throughout the life of each female (see Mackintosh 1942). Thus the number of ovulations that has occurred in a female may be counted. Such counts have been used as an index of relative age (Pike 1953; Chittleborough 1955*b*). If the number of ovulations is recorded for each individual in a large sample of females, the frequency distribution of these ovulation counts may be used as a measure of the age distribution within that sample.

This has been applied to the female humpback whales taken in Australian waters. Table 7 summarizes the distribution of the numbers of ovulations that occurred in females sampled at random from catches on the Western Australian coast. For convenience the ovulation counts have been arbitrarily grouped, generally in units of three. No attempt will be made here to fix the absolute age within each of these groups, but the frequency distributions given in Table 7 do give a measure of the relative age distribution of the females sampled from season to season.

Figure 5 shows these results in histogram form. Assuming that the samples were representative of the females taken in each year, the following deductions can be made. In 1951 and 1952, the younger age groups amongst the sexually mature females (i.e., 1—6 ovulations) dominated the catches of females. In 1953 and 1954 there was a decline in the relative age distribution so that immature (0 group) and recently mature (1—3 ovulations) females were predominant while the proportions of slightly older whales (4—9 ovulations) decreased. Relatively old females (16—18 ovulations and those with over 18 ovulations) were never abundant and showed little change over these four years.

This evidence of a decline in the relative age distribution as indicated by ovulation counts is quite independent of the evidence from the analysis of catch returns kept by whaling inspectors, and confirms that up to 1954 there had been a decline in the composition of the catch.

In 1956 the frequency distribution of ovulation counts showed a marked improvement. The proportions of relatively old females (16—18 ovulations and those with over 18 ovulations) remained almost unchanged, but the youngest group of whales (0 group) decreased very considerably while the middle age classes (4—15 ovulations) increased. This can be interpreted as the result of the more stringent selection of larger individuals which is known to have been applied in 1956.

(g) Pregnancy.

Table 8 shows the number and percentages of females in advanced pregnancy amongst the sexually mature females taken in yearly catches of individual stations on the Western Australian coast and also amongst the sexually mature females in seasonal catches from Antarctic Area IV over the corresponding period. It is immediately obvious that fewer females in advanced pregnancy are taken in warmer waters than in Antarctic regions (see also Table 15 for the Group V stock). This is because pregnant females in the Antarctic are in approximately mid-pregnancy, while those along the Australian coast carry near-term foetuses and a considerable number of calves are born before the females reach the northern whaling areas.

In some females taken at Western Australian coastal stations, conception has only recently occurred, but the early embryos are seldom located and few of these females are recorded as pregnant. For this reason there has been no attempt to include females in early pregnancy in Table 8.

There have been fairly consistent differences in the frequency of advanced pregnancy in the catches at each of the three areas on the Western Australian coast where humpback whaling has been carried out. The southern-most station (near Albany) operating upon whales which have most recently arrived from Antarctic waters, generally takes the highest percentage of late-pregnant females. However, as this station has a small annual quota, the actual number of late-pregnant females taken is not disturbing when compared with Antarctic catches of pregnant females.

In the more northerly regions of Carnarvon and Point Cloates, relatively fewer females in advanced pregnancy are taken. A lower proportion of late-pregnant females is taken off Carnarvon than at Point Cloates, apparently due to differences in the local conditions.

(h) Discussion and Conclusions regarding the Group IV Stock of Humpback Whales.

There is considerable evidence both from the Western Australian coast and from Antarctic Area IV that from 1949 to 1954 there was a decline in the composition of the catches of humpback whales. Since the degree of selection had remained at comparable levels from year to year, this decline in the composition of the catches may logically be interpreted as reflecting a deterioration in the condition of this stock of humpback whales.

In 1955, after a reduction of the quotas on the Western Australian coast, the composition of the catch in that region improved very considerably. There can be little doubt that this improvement was mainly due to the much higher degree of selection that is known to have been applied in that year.

In 1956 the constitution of the catch on the Western Australian coast was more favourable than that of the 1955 season. There was a similar stringent selection of larger whales in 1956 as in 1955. As a result of the closing of the station at Point Cloates in 1956 and the transfer of that station's quota, catching vessels, and some factory equipment to the Carnarvon station, the selection factor could be applied more effectively. Further, local conditions in the Carnarvon area afford more advantages for whaling than Point Cloates (for example, the lower proportion of females and lower percentage of mature females in advanced pregnancy).

The composition of the catch in Antarctic Area IV during 1956 showed a little improvement in some (but not all) aspects when compared with the catch in 1954, but the 1956 catch does not compare favourably with the composition of the corresponding catch on the Western Australian coast. This suggests that the Group IV stock as a whole has not yet recovered from its earlier decline.

The success of the more careful selection of larger individuals, applied on the Western Australian coast in the last two seasons, suggests that the Group IV stock is capable of being conserved at an economic level if the total annual catch is not increased and if selection is maintained at a high level.

III. GROUP V.

(a) General.

In the following sections when considering trends within the recent catches of humpback whales from Antarctic Area V, the illegal catch reported to have been taken by the factory ship «Olympic Challenger» in 1955 has been omitted. Between January 5 and March 7, 1955, this factory ship apparently took a total of 1125 humpback whales in Antarctic waters. Of these, 1097 were taken in Antarctic Area V and 28 from Area IV. But only 170 humpback whales (from Antarctic Area V) were reported to the International Whaling Statistics (see The Norwegian Whaling Gazette, August 1955, p. 446). These 170 whales are included in the statistics of Tables 9—13 and Table 15 of the present report. Although the remainder of this vessel's catch for 1955 is not shown in the following analyses, the possible effects of this large catch of poorly selected whales should be noted when considering the state of the Group V stock in relation to fishing intensity.

In the analysis of catch returns of humpback whales taken in warmer regions of the Group V stock, the records from the station on Norfolk Island have been kept separate from those of the stations on the eastern coast of Australia (at Tangalooma and Byron Bay). This is being done while the movements and dispersal of humpback whales in the south-west Pacific region are being investigated. Although humpback whales considered as the Group V stock may presumably mingle in Antarctic waters, it is possible (but not proven) that individual whales follow fairly similar courses each year in their northward migration. For example, some may return to the eastern coast of Australia each winter and so be isolated to some extent from those which pass New Zealand and the islands to the north. The small station at Norfolk Island affords an excellent opportunity to study this point.

(b) Sex Ratio.

The sex ratio in the yearly catches of individual and combined stations on the eastern Australian coast, of Norfolk Island, and of seasonal catches in Antarctic Area V (from the 1949/50 season) is shown in Table 9. In this stock of humpback whales females continue to predominate in Antarctic catches while males constitute the greater part of catches made in warmer waters.

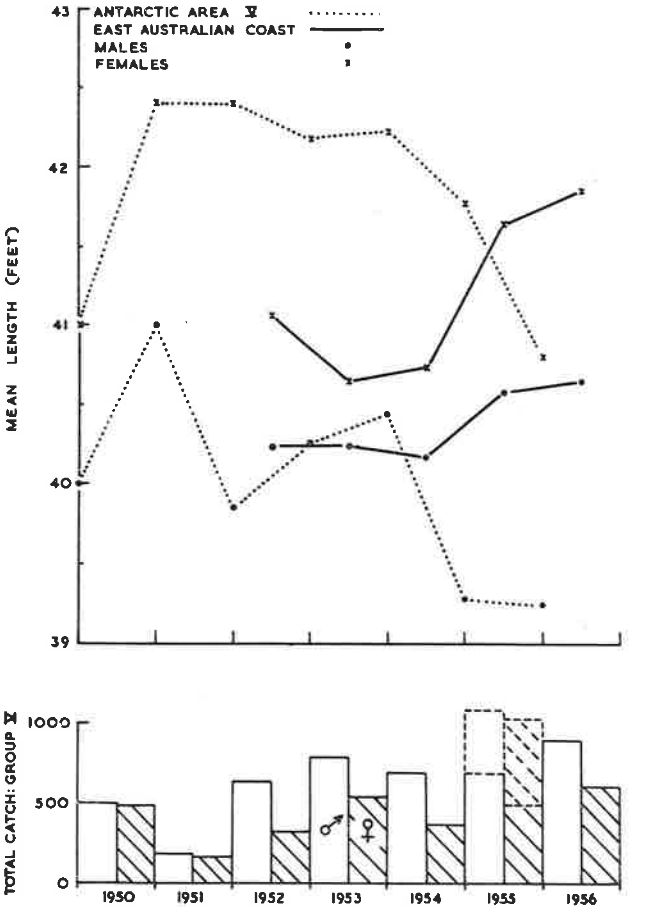
On the eastern Australian coast, the proportion of females in the catch has increased slightly but fairly regularly from 1952 to 1956. In some years this increase may be related to a change in the period of whaling operations (for example the earlier catching at Byron Bay in 1955 than in 1954), but in addition this steady increase in the percentage of females might be due to an increase in the selection of larger whales (females generally being larger than males).

(c) Mean Lengths.

Table 10 lists the mean lengths of males and females in yearly catches of individual and combined stations on the eastern Australian coast, of Norfolk Island, and of seasonal catches in Antarctic Area V from 1950. The mean lengths for both sexes in yearly catches from the eastern Australian coast and from Antarctic Area V are plotted in Figure 6. Also shown in Figure 6 are the total numbers of males and females taken from the Group V stock in each year from 1950 to 1956. These totals include catches from the eastern Australian coast, Norfolk Island, New Zealand, and Antarctic Area V, indicating also the catch of 927 humpback whales reported to have been taken illegally from this stock in 1955.

In the case of the males, Figure 6 shows that from 1952 to 1954 the mean lengths of the males from the eastern Australian coast were similar to those from Antarctic Area V. In 1955 and 1956 the mean lengths of the males from Antarctic Area V fell considerably, yet in these years on the eastern Australian coast the mean lengths of the males increased.

With the females the change in recent years has been even more marked. Figure 6 shows that from 1952 to 1954 the mean lengths of the females taken on the eastern Australian coast were considerably below those from Antarctic Area V. But from 1955 to 1956 this condition was reversed as the mean length of females from the eastern Australian coast increased and that from Antarctic Area V declined.



*Broken portion indicating the catch of 927 humpback whales reported to have been taken illegally from this stock (not included in mean lengths).

Fig. 6.- Above: Mean lengths of males and females in seasonal catches of combined Eastern Australian coast stations and of Antarctic Area V. Below: Total catches of males and females from the Group V stock in each year from 1950 to 1956.

(d) Length Frequencies.

Table 11 shows the length frequency distribution of males in yearly catches on the eastern Australian coast from 1952 to 1956, on Norfolk Island in 1956, and from Antarctic Area V from 1950 to 1956. It also shows that in 1955 and 1956 there was a slight improvement in the length frequency distribution of males taken on the eastern Australian coast, the proportions of males in the smaller length ranges decreasing. At the same time catches of males from Antarctic Area V showed an increase in the proportions of males in the lower length groups.

Table 12 shows corresponding records for the females in the catches. This table shows that for females on the eastern Australian coast there was a slightly poorer length frequency distribution in 1954, some improvement in 1955, and a definite trend towards the upper length ranges in 1956. In Antarctic Area V the length frequency distribution of females in the catches showed relatively minor fluctuations up to 1954, but swung towards the lower length ranges in 1955 and 1956.

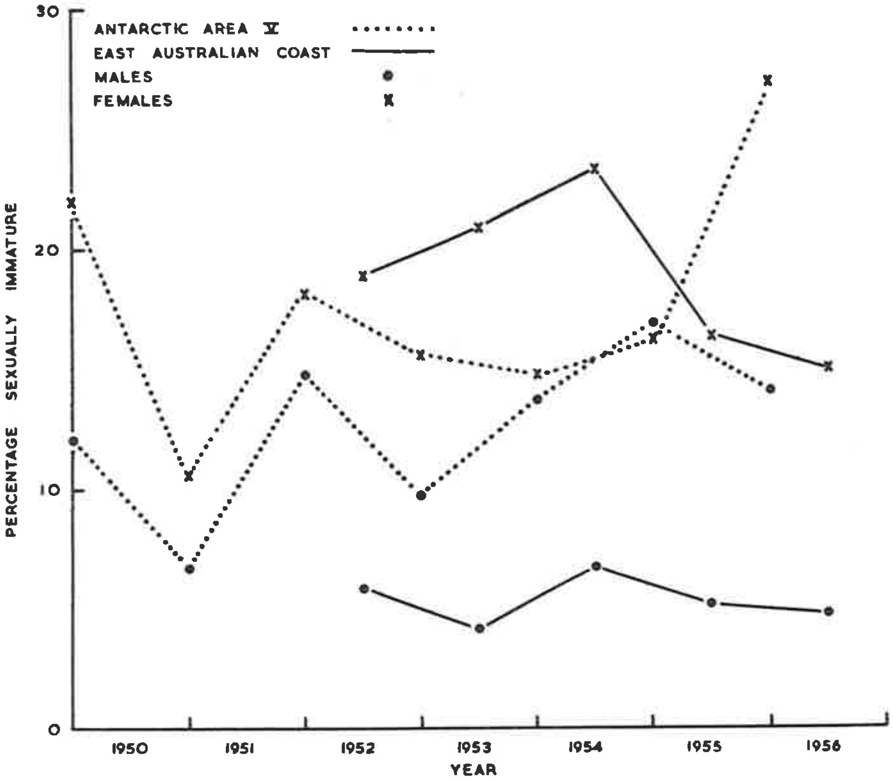


Fig. 7.- Percentages of sexually immature males and females in yearly catches of combined Eastern Australian coast stations and of Antarctic Area V.

(e) Sexually Immature Whales.

Using the same criteria for immaturity as for the Group IV humpback whales, Table 13 shows the numbers and percentages of sexually immature males and females in the yearly catches from individual and combined catches on the eastern Australian coast, from Norfolk Island, and from Antarctic Area V from 1950 to 1956. Figure 7 shows the percentages of immature males and females in the annual catches from the eastern Australian coast and from Antarctic Area V.

Considering first the males, Figure 7 shows that on the eastern Australian coast the percentage of immature males in the yearly catch has remained very low, with relatively slight fluctuations, from 1952 to 1956. In catches from Antarctic Area V the percentage of immature males has been higher and fluctuated more, but reached its highest level in 1955, falling slightly in 1956. In general the percentages of immature males in catches from Antarctic Area V have been lower than from corresponding catches in Antarctic Area IV (cf. Figs. 4 & 7).

In the case of the females, Figure 7 shows that on the eastern Australian coast the percentage of immature females rose to a peak in 1954 but decreased considerably in 1955 and continued to fall slightly in 1956. In Antarctic Area V the percentage of immature females, initially lower than on the eastern Australian coast, increased greatly in 1956. These recent changes in the percentages of immature females in catches from the eastern Australian coast and from Antarctic Area V are reciprocal to the changes in the mean lengths of females in the same catches (cf. Figs. 6 & 7).

(f) Ovulation counts as an index of the relative age distribution in the catches of females.

On the same basis as described for the Group IV stock (Section II (f)), Table 14 summarizes the distribution of the numbers of ovulations that had occurred in females sampled at random from the catches at the Tangalooma station. Figure 8 shows these results in histogram form. Assuming that the samples were representative of the females taken on the eastern Australian coast each year, they afford some measure of changes in the age distribution within the catches. On this evidence Figure 8 indicates that in 1952 and 1953 the age distribution of the females taken on the eastern Australian coast was similar, except that fewer old females (16—18 ovulations and those with more than 18 ovulations) were taken in 1953 (and in succeeding years).

In 1954 there was a marked swing towards younger females in the catch, the group 0 (immature) and 1—3 ovulations (recently matured) increasing at the expense of the slightly older females (groups with 4—6 and 7—9 ovulations). This is consistent with the poorer length frequency distribution in females from the eastern Australian coast in 1954 (Table 12), and the higher proportion of immature females (Fig. 7).

In 1955 the age composition of the females (as indicated by ovulation counts) improved, but had not returned to the condition of earlier years (1952 and 1953). The distribution of ovulation counts for 1956 indicated that the age distribution of the females in the catch on the eastern Australian coast improved considerably, being more favourable than in any previous year. Younger whales (group 0)

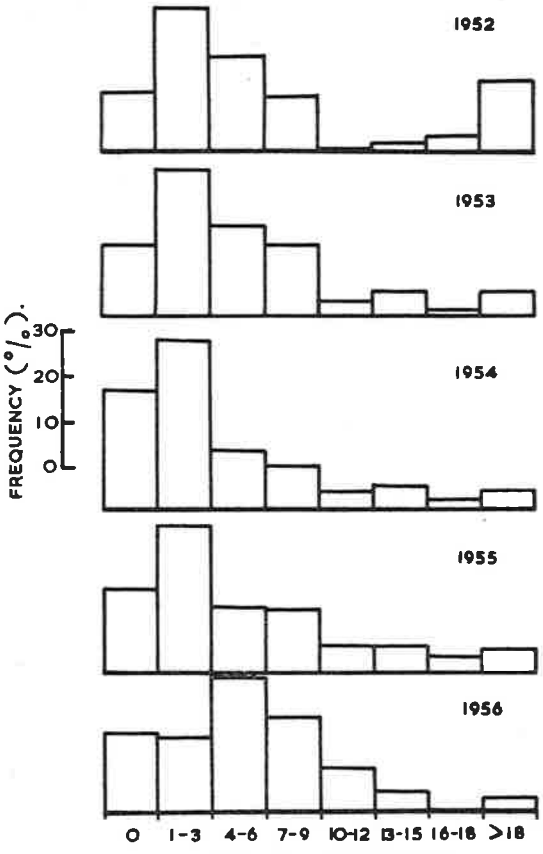


Fig. 8.- Relative age distribution (based on ovulation counts) of females sampled from catches on the Eastern Australian coast (Tangalooma).

were still evident, but relatively older whales (groups with 4—6 and 7—9 ovulations) dominated the catch. This improvement in the age distribution would be consistent with a more careful selection of larger individuals.

(g) Pregnancy.

Table 15 shows the numbers and percentages of females in advanced pregnancy amongst the sexually mature females in yearly catches at individual stations on the eastern Australian coast from 1952 to 1956, and from Antarctic Area V from 1950 to 1956. No females in advanced pregnancy were taken at Norfolk Island in 1956.

As discussed earlier in the case of the Group IV stock, more pregnant females were taken in the Antarctic than in the warmer northern waters, but in the latter region additional females (not included in Table 15) would be in very early stages of pregnancy. In the catches on the eastern coast of Australia the percentages of females in advanced pregnancy fluctuate each year, but about different levels at each station. Similar differences between the percentages of pregnant females at individual stations are found on the Western Australian coast (Table 8).

(h) Discussion and Conclusions Regarding the Group V Stock of Humpback Whales.

In its first season of operation, the catch taken by the station on Norfolk Island compared very favourably with the 1956 catch on the eastern coast of Australia. Some aspects, for example the mean length of the males and the length frequency distribution of the males, were better than on the eastern coast of Australia. The percentage of females was slightly higher at Norfolk Island, as was the percentage of immature females, but neither of these features was very adverse.

On the eastern Australian coast, the 1954 catch of females contained some unfavourable trends, i.e., from the evidence of lengths, a slightly poorer length frequency distribution and more immature individuals, and on the evidence of ovulation counts, a marked swing towards young individuals. Increased mean lengths of both males and females, more favourable length frequency distribution in both sexes, the taking of fewer immature females, the improvement in the age distribution of females based on evidence from ovulation counts indicate a considerable improvement in the catch composition of whales taken in 1955 and 1956 on the eastern Australian coast. It may be remembered that, just prior to the 1955 season, there was a reduction in the quota of whales to be taken on the western Australian coast. It is suggested that this reduction in the West has stimulated a more careful selection of larger individuals on the east coast in 1955 and 1956.

In contrast, the composition of the catches in Antarctic Area V considerably declined in 1955 and 1956; the mean lengths of both males and females decreased, the length frequency distribution swung towards the lower length ranges in both sexes, and the proportion of immature females rose greatly. Unless it can be proved that there was far less selection of whales in Antarctic Area V during the 1954/55 and 1955/56 seasons than in previous seasons, these trends in the catches of the last two years may be interpreted as reflecting a slight decline in the condition of the Group V stock of humpback whales. The large catch reported to have been taken illegally during 1955 in Antarctic Area V by the factory ship «Olympic Challenger», when superimposed upon all other humpback whales taken in that year from the Group V stock (see Fig. 6) could have played a part in causing this apparent decline.

Although more evidence is required from catches in the immediate future, it appears that the Group V stock will not withstand continuous fishing at any higher level than that allowed at present.

IV. COMPARISON OF HUMPBACK WHALING IN ANTARCTIC AND TEMPERATE WATERS.

From the analyses of recent catches from the Group IV and V stocks of humpback whales as given in this report, the following comparison is made between the composition of catches in Antarctic and Australian waters.

(1) *Sex ratio.* — Catches on the Western Australian coast generally contain a lower proportion of females than catches in Antarctic Area IV (Table 2). Catches on the eastern Australian coast always contain far lower proportions of females than in Antarctic Area V (Table 9).

(2) *Mean length of males.* — The mean lengths of the males in the catches are generally higher on the Western Australian coast than in Antarctic Area IV (Fig. 3), and in recent years (1955 and 1956) higher on the eastern Australian coast than in Antarctic Area V (Fig. 6).

(3) *Mean length of females.* — The mean lengths of the females in the catches are usually higher on the Western Australian coast than in Antarctic Area IV (Fig. 3), but lower on the eastern Australian coast than in Antarctic Area V, except for the 1956 catches (Fig. 6).

(4) *Percentage of immature males.* — There are generally considerably lower proportions of immature males in Australian catches than in Antarctic catches (Figs. 4 & 7).

(5) *Percentage of immature females.* — The percentages of immature females are lower in catches on the Western Australian coast than in Antarctic Area IV (Fig. 4), but higher in catches on the eastern Australian coast than in Antarctic Area V, except for the 1956 catches (Fig. 7).

(6) *Pregnancy.* — Catches from the Antarctic contain far higher proportions of females in advanced pregnancy than catches in Australian waters (Tables 8 and 15). Two points should be stressed here. Firstly, some females taken in Australian waters having recently conceived may not have been recorded as pregnant. Secondly, the proportions of pregnant females recorded in Antarctic catches (e.g. in Tables 8 and 15) should be regarded as minimal, since much higher proportions of mature females in Antarctic waters were found to be pregnant when carefully examined by Norwegian observers (Chittleborough 1957).

In an evaluation of the aspects given above, it would appear more favourable (from the point of the conservation of the humpback stocks) to take these whales in temperate regions rather than in Antarctic waters. It may be argued that the whales are fatter in the southern feeding grounds, but this is compensated for by the efficiency and lower running costs of shore stations; storage space is available for more complete extraction of whale meal and dehydrated whale solubles.

Some of the aspects of the catch composition which are more favourable on the Australian coast may be largely due to the more careful selection of the larger whales. The fixed quotas allotted to individual stations on the Australian coast reduce the competition between stations, encouraging more careful selection to be applied and also more efficient treatment, so that production per whale may approach an optimum. In contrast, for the Antarctic factory ship, speed of catching and processing is vital under the present system to ensure the highest proportion of the Antarctic catch. These factors do not lead to the best utilization of the remaining stocks of whales.

TABLE 1.

Western Australian Coast.
Average Catching Rates at Point Cloates & Carnarvon
in seasonal Catches.

POINT CLOATES

Year	Date of Opening	Date of Closing	Total days	Total catch	Avge. no. whales per day	No. catchers	No. of catcher days	Avge. no. of whales/ catcher/ day
1950	June 29	Oct. 9	103	348	3.38	2*	162	2.15
1951	June 21	Oct. 14	116	574	4.95	3*	211	2.72
1952	June 23	Oct. 9	109	536	4.92	3*	232	2.31
1953	June 10	Sept. 15	98	600	6.12	3*	269	2.23
1954	June 14	Sept. 15	94	600	6.38	3	282	2.13
1955	June 27	Sept. 19	85	500	5.88	3	255	1.96
CARNARVON								
1951	June 25	Oct. 9	107	650	6.07	3*	286	2.27
1952	June 2	Sept. 1	92	600	6.52	3*	196	3.06
1953	June 8	Sept. 6	91	600	6.59	3*	143	4.19
1954	June 8	Aug. 31	85	600	7.06	2	170	3.53
1955	June 8	Aug. 26	80	500	6.25	2	160	3.12
1956	June 12	Sept. 22	103	1000	9.71	5*	508	1.97

* One or more catchers not used for full season.

TABLE 2.

Humpback Whales: Group IV.
Sex Ratio in seasonal Catches 1949—1956.

WESTERN AUSTRALIAN COAST

Station	Year	Total Catch	Sex unknown	No. Males	No. Females	% Females
Point Cloates	1949	190	—	135	55	28.9
	1950	348	1	212	135	38.8
	1951	574	4	386	184	32.3
	1952	536	5	283	248	46.7
	1953	600x	5	306	289	48.2
	1954	600	11	271	318	54.0
	1955	500	2	228	270	54.2
Carnarvon	1950	40	—	38	2	5.0
	1951	650	3	521	126	19.5
	1952	600	—	360	240	40.0
	1953	600	—	367	233	38.8
	1954	600	—	353	247	41.2
	1955	500	—	272	228	45.6
	1956	1000	—	617	383	38.3
Albany	1952	51	—	23	28	54.9
	1953	100	—	53	47	47.0
	1954	120	—	68	52	43.3
	1955	120*	—	80	40	33.3
	1956	119	—	59	60	50.43
All Western Australian Coast Stations	1949	190	—	135	55	28.9
	1950	388	1	250	137	34.9
	1951	1224	7	907	310	25.5
	1952	1187	5	666	516	43.7
	1953	1300x	5	726	569	43.9
	1954	1320	11	692	617	47.1
	1955	1120*	2	580	538	48.1
	1956	1119	—	676	443	39.6
ANTARCTIC AREA IV						
	1949/50	779	—	354	425	54.6
	1950/51	1112	—	468	644	57.9
	1951/52	1127	—	546	581	51.6
	1952/53	193	—	103	90	46.6
	1953/54	258	—	133	125	48.4
	1954/55	0	—	—	—	—
	1955/56	824	—	320	504	61.2

x Excluding three taken under special licence for research purposes.
* Excluding six taken under special licence for research purposes.

TABLE 3.

Humpback Whales: Group IV.
Mean Lengths (Feet) of Males and Females in seasonal Catches
1949—1956.

WESTERN AUSTRALIAN COAST

Station	Year	Males		Females	
		No.	Mean length	No.	Mean length
Point Cloates	1949	135	40.36	55	41.43
	1950	212	39.86	135	41.13
	1951	386	39.99	184	40.89
	1952	283	39.94	248	41.26
	1953	306	39.14	289	40.73
	1954	271	38.90	318	40.15
	1955	228	39.33	270	41.19
Carnarvon	1950	38	41.50	2	41.00
	1951	521	40.16	126	40.92
	1952	360	39.44	240	41.25
	1953	367	38.90	233	40.68
	1954	353	38.54	247	40.75
	1955	272	40.37	228	42.45
	1956	617	40.52	383	42.38
Albany	1952	23	40.74	28	43.17
	1953	53	39.52	47	40.25
	1954	68	39.43	52	41.44
	1955	80	39.73	40	41.14
	1956	59	38.53	60	41.95
All Western Australian Coast Stations	1949	135	40.36	55	41.43
	1950	250	40.10	137	41.15
	1951	907	40.11	310	40.92
	1952	666	39.48	516	41.35
	1953	726	39.05	569	40.67
	1954	692	38.77	617	40.50
	1955	580	39.88	538	41.72
	1956	676	40.35	443	42.32
ANTARCTIC AREA IV					
	1949/50	354	39.48	425	41.14
	1950/51	468	39.44	644	41.22
	1951/52	546	39.00	581	40.72
	1952/53	103	38.11	90	40.26
	1953/54	133	38.83	125	39.72
	1954/55	0	—	—	—
	1955/56	320	38.78	504	40.52

TABLE 4.

Humpback Whales: Group IV.
Length Frequencies in seasonal Catches.
Males.

Length	WESTERN AUSTRALIAN COAST							ANTARCTIC AREA IV						
(feet)	1950	1951	1952	1953	1954	1955	1956	1949 /50	1950 /51	1951 /52	1952 /53	1953 /54	1954 /55	1955 /56
27	—	—	—	—	—	—	—	—	—	—	—	—		—
28	—	—	—	—	—	—	—	—	—	2	—	—		—
29	—	—	—	—	—	—	—	—	—	—	—	—		—
30	—	—	1	—	1	—	—	2	3	2	1	—		—
31	1	—	—	—	—	—	—	—	1	1	—	—		1
32	2	—	1	4	—	—	—	2	5	7	1	—		—
33	—	5	3	4	—	—	2	4	10	13	5	—		—
34	—	—	5	1	—	1	—	8	4	2	—	—		1
35	5	17	38	49	46	16	11	19	11	68	10	11		14
36	10	38	36	62	72	27	28	31	38	46	12	9	NONE TAKEN	35
37	15	64	71	84	87	35	30	34	57	40	14	19		53
38	16	81	72	112	127	60	55	22	40	43	19	24		48
39	38	133	106	111	113	98	78	36	55	63	13	24		42
40	51	167	97	96	84	133	131	58	62	74	9	19		58
41	41	167	88	66	61	63	114	40	60	62	5	8		34
42	41	108	66	68	51	69	102	46	56	52	6	11		16
43	17	72	52	28	23	42	72	25	33	28	4	3		8
44	8	37	18	21	18	19	29	16	15	21	2	3		8
45	4	15	8	16	6	12	18	8	17	13	1	—		2
46	1	3	3	4	3	4	2	2	—	5	—	1		—
47	—	—	1	—	—	1	3	1	1	3	1	1		—
48	—	—	—	—	—	—	1	—	—	—	—	—		—
49	—	—	—	—	—	—	—	—	—	1	—	—		—
50														
	250	907	666	726	692	580	676	354	468	546	103	133	0	320

TABLE 5.

Humpback Whales: Group IV.
Length Frequencies in seasonal Catches.
Females.

Length	WESTERN AUSTRALIAN COAST							ANTARCTIC AREA IV						
(feet)	1950	1951	1952	1953	1954	1955	1956	1949 /50	1950 /51	1951 /52	1952 /53	1953 /54	1954 /55	1955 /56
27	—	—	—	—	—	—	—	—	—	2	—	—	NONE TAKEN	—
28	—	—	—	—	—	—	—	—	—	—	—	—		—
29	—	—	1	1	—	1	—	2	1	1	—	—		—
30	—	—	1	2	—	—	—	1	1	1	—	2		—
31	—	—	1	1	—	—	—	—	1	5	—	—		1
32	1	—	—	1	1	—	1	4	5	4	—	1		2
33	—	1	1	—	3	2	1	6	9	8	3	—		—
34	1	1	—	—	—	—	—	3	4	3	—	—		—
35	4	12	17	36	42	7	6	11	15	52	7	11		15
36	9	9	27	33	48	13	11	13	26	32	3	5		43
37	8	25	31	41	46	20	7	18	28	24	7	11		37
38	7	26	21	58	62	37	13	27	50	29	10	18		40
39	10	27	43	51	53	48	33	38	47	48	8	13		46
40	16	38	48	47	63	70	58	45	48	58	9	18		63
41	12	33	61	53	42	54	37	36	69	52	10	12		65
42	21	36	62	55	53	58	48	62	97	54	13	9		60
43	15	38	62	51	61	60	53	47	79	54	5	8		39
44	9	29	53	57	57	54	68	49	71	43	3	5		38
45	11	17	36	27	33	39	43	32	35	40	4	4		24
46	9	10	27	29	32	38	26	15	28	37	3	5		23
47	2	4	14	17	9	23	20	11	18	18	1	—		7
48	2	2	7	8	7	9	10	4	10	10	4	2		1
49	—	1	1	1	3	3	7	1	2	2	—	—		—
50	—	1	2	—	1	2	1	—	—	2	—	1		—
51	—	—	—	—	—	—	—	—	—	2	—	—		—
52	—	—	—	—	1	—	—	—	—	—	—	—		—
	137	310	516	569	617	538	443	425	644	581	90	125	0	504

TABLE 6.
Humpback Whales: Group IV.
Sexually immature in seasonal Catches
1949 — 1956

WESTERN AUSTRALIAN COAST

Station	Year	Males			Females		
		Total	Immature		Total	Immature	
		No.	No.	%	No.	No.	%
Point Cloates	1949	135	4	2.95	55	13	23.64
	1950	212	18	8.49	135	30	22.22
	1951	386	28	7.25	184	46	25.00
	1952	283	36	12.72	248	56	22.58
	1953	306	45	14.71	289	87	30.10
	1954	271	55	20.30	318	127	39.94
	1955	228	32	14.04	270	64	23.70
Carnarvon	1950	38	—	0	2	0	0
	1951	521	32	6.14	126	28	22.22
	1952	360	45	12.50	240	42	17.50
	1953	367	81	22.01	233	70	30.04
	1954	353	68	19.26	247	71	28.74
	1955	272	6	2.21	228	12	5.26
	1956	617	33	5.35	383	35	9.14
Albany	1952	23	1	4.35	28	0	0
	1953	53	10	18.87	47	18	38.30
	1954	68	13	19.12	52	11	21.15
	1955	80	11	13.75	40	12	30.00
	1956	59	13	22.03	60	10	16.67
All Western Australian Coast Stations	1949	135	4	2.95	55	13	23.64
	1950	250	18	7.20	137	30	21.90
	1951	907	60	6.62	310	74	23.87
	1952	666	82	12.31	516	98	18.99
	1953	726	136	18.73	569	175	30.76
	1954	692	136	19.65	617	209	33.87
	1955	580	49	8.45	538	88	16.36
	1956	676	46	6.80	443	45	10.16
ANTARCTIC AREA IV							
	1949/50	354	66	18.64	425	85	20.00
	1950/51	468	72	15.38	644	140	21.75
	1951/52	546	141	25.82	581	161	27.71
	1952/53	103	29	28.16	90	30	33.33
	1953/54	133	20	15.04	125	48	38.40
	1954/55	0	—	—	0	—	—
	1955/56	320	51	15.94	504	138	27.38

TABLE 7.
Frequency Distribution of Ovulation Counts from Female Humpback Whales in recent Catches on the Western Australian Coast.

Year		1951	1952	1953	1954	1955	1956
No. of pairs of ovaries examined		92	274	244	122	*	279
Ovulation counts. — % frequency distribution	0	17.4	17.9	29.1	27.9		8.6
	1— 3	31.5	24.5	28.7	25.4		28.7
	4— 6	20.7	22.6	12.3	14.8		19.4
	7— 9	13.0	13.9	12.3	8.2		10.4
	10—12	7.6	6.2	4.1	9.8		11.8
	13—15	2.2	2.6	3.3	4.1		10.4
	16—18	4.3	3.3	2.5	1.6		2.9
	> 18	3.3	9.1	7.8	8.2		7.9

* 1955 Sample selected: not representative.

TABLE 8.
Humpback Whales: Group IV
Females in advanced Pregnancy from seasonal Catches.

WESTERN AUSTRALIAN COAST

Station	Year	No. of mature females	Females in advanced pregnancy	
			No.	Percentage
Point Cloates	1949	42	3	7.1
	1950	105	23	21.9
	1951	138	13	9.4
	1952	192	38	19.8
	1953	202	49	24.3
	1954	191	27	14.1
	1955	206	14	6.8
Carnarvon	1951	98	5	5.1
	1952	198	7	3.5
	1953	163	16	9.8
	1954	176	11	6.3
	1955	216	1	0.5
	1956	348	25	7.2
Albany	1952	28	11	39.3
	1953	28	12	42.9
	1954	41	18	43.9
	1955	28	1	3.6
	1956	50	13	26.0
Total 1949—1956		2450	287	11.7
ANTARCTIC AREA IV				
	1949/50	340	169	49.7
	1950/51	504	303	60.1
	1951/52	420	152	36.2
	1952/53	60	40	66.7
	1953/54	77	32	41.6
	1954/55	0	—	—
	1955/56	366	155	42.3
Total 1950—1956		1767	851	48.2

TABLE 9.

Humpback Whales: Group V.
Sex Ratio in seasonal Catches.

EASTERN AUSTRALIAN COAST

Station	Year	Total Catch	Sex unknown	No. Males	No. Females	% Females
Tangalooma	1952	600	1	449	150	25.1
	1953	700	—	509	191	27.3
	1954	598	—	420	178	29.8
	1955	600	—	429	171	28.5
	1956	600	—	407	193	32.2
Byron Bay	1954	120	—	91	29	24.2
	1955	120	—	65	55	45.5
	1956	120	—	78	42	35.0
All Eastern Australian Coast Stations	1952	600	1	449	150	25.1
	1953	700	—	509	191	27.3
	1954	718	—	511	207	28.8
	1955	720	—	494	226	31.4
	1956	720	—	485	235	32.6
Norfolk Is.	1956	150	—	92	58	38.7
ANTARCTIC AREA V						
	1949/50	903	—	441	462	51.2
	1950/51	228	—	105	123	53.9
	1951/52	183	—	67	116	63.4
	1952/53	516	—	215	301	58.3
	1953/54	150	—	75	75	50.0
	1954/55	348	—	124	224	64.4
	1955/56	467	—	222	245	52.5

TABLE 10.

Humpback Whales: Group V.
Mean Length (Feet) of Males and Females in seasonal Catches.

EASTERN AUSTRALIAN COAST

Station	Year	Males		Females	
		No.	Mean length	No.	Mean length
Tangalooma	1952	448	40.25	150	41.06
	1953	509	40.25	191	40.66
	1954	420	40.13	178	40.57
	1955	429	40.46	171	41.30
	1956	407	40.63	193	41.73
Byron Bay	1954	91	40.34	29	41.84
	1955	65	41.54	55	42.77
	1956	78	40.74	42	42.40
All Eastern Australian Coast Stations	1952	448	40.25	150	41.06
	1953	509	40.25	191	40.66
	1954	511	40.17	207	40.74
	1955	494	40.59	226	41.66
	1956	485	40.65	235	41.85
Norfolk Is.	1956	92	41.31	58	42.09
ANTARCTIC AREA V					
	1949/50	441	40.01	462	41.00
	1950/51	105	41.00	123	42.41
	1951/52	67	39.86	116	42.41
	1952/53	215	40.27	301	42.19
	1953/54	75	40.46	75	42.23
	1954/55*	124	39.29	224	41.77
	1955/56	222	39.25	245	40.80

* Excluding 927 humpback whales reported to have been taken illegally.

TABLE 11.
Humpback Whales: Group V.
Length Frequencies in seasonal Catches.
Males.

Length	EASTERN AUSTRALIA Coastal					Norfolk Island	ANTARCTIC AREA V						
(feet)	1952	1953	1954	1955	1956	1956	1949 /50	1950 /51	1951 /52	1952 /53	1953 /54	1954 /55	1955 /56
25	—	—	—	—	—	—	3	—	—	—	—	—	—
26	—	—	—	—	—	—	—	—	—	—	—	—	—
27	—	—	—	—	—	—	—	—	—	—	—	—	—
28	—	—	—	—	—	—	—	—	—	—	—	—	—
29	—	—	—	—	—	—	—	—	1	—	—	—	—
30	—	—	1	—	1	—	1	1	—	—	—	—	—
31	1	1	—	—	—	—	—	—	—	—	—	—	—
32	1	—	1	—	1	—	5	—	—	1	1	1	—
33	1	—	1	2	2	—	7	1	—	3	—	1	1
34	1	2	—	1	—	—	3	—	—	1	—	1	4
35	6	9	18	10	7	2	16	2	6	4	3	12	11
36	15	9	13	13	11	4	20	3	3	12	6	6	15
37	20	31	18	21	22	4	27	4	3	18	5	11	24
38	42	50	59	32	25	3	26	9	6	20	4	16	37
39	65	75	75	55	56	6	55	4	3	20	3	14	25
40	77	76	89	92	97	8	73	13	11	33	11	21	36
41	86	94	78	79	82	16	60	22	11	24	13	9	28
42	71	89	78	82	81	17	62	16	6	39	9	17	19
43	40	56	47	66	51	15	38	8	3	11	11	9	11
44	15	14	19	30	27	11	21	13	7	16	6	4	6
45	6	3	11	7	15	3	17	7	6	8	1	2	4
46	1	—	3	3	6	2	3	1	1	2	1	—	—
47	—	—	—	1	—	1	4	1	—	1	—	—	1
48	—	—	—	—	1	—	—	—	—	1	1	—	—
49	—	—	—	—	—	—	—	—	—	—	—	—	—
50	—	—	—	—	—	—	—	—	—	1	—	—	—
	448	509	511	494	485	92	441	105	67	215	75	124	222

TABLE 12.

Humpback Whales: Group V.
Length Frequencies in seasonal Catches.
Females.

Length	EASTERN AUSTRALIA Coastal					Norfolk Island	ANTARCTIC AREA V						
(feet)	1952	1953	1954	1955	1956	1956	1949 /50	1950 /51	1951 /52	1952 /53	1953 /54	1954 /55	1955 /56
27	—	—	—	—	—	—	—	—	—	—	—	—	—
28	—	—	—	—	—	—	1	—	—	—	—	—	—
29	—	—	—	—	—	—	—	—	—	—	—	—	—
30	—	—	—	—	—	—	1	—	—	1	—	—	—
31	—	—	—	—	—	—	6	—	—	—	—	—	—
32	1	2	3	—	—	—	5	—	1	—	—	1	—
33	—	2	4	—	1	—	6	—	—	1	—	—	2
34	—	1	—	—	1	—	3	—	—	—	—	—	1
35	5	7	9	7	3	4	19	2	5	11	2	3	5
36	5	11	4	3	4	1	17	4	3	11	2	6	14
37	11	7	6	12	15	4	11	4	4	13	3	16	17
38	6	11	20	13	10	3	33	3	8	10	4	10	27
39	15	21	28	21	11	3	26	5	3	13	1	22	21
40	14	11	16	27	22	6	48	10	4	29	7	23	28
41	20	29	31	22	23	4	54	17	9	17	9	21	25
42	22	34	24	27	30	5	61	15	12	48	13	31	23
43	21	32	19	27	42	5	57	11	16	32	10	23	31
44	14	12	17	23	34	4	50	23	15	34	4	16	20
45	10	5	8	22	20	4	28	12	16	32	5	21	18
46	1	1	12	9	9	6	20	10	11	25	10	14	5
47	4	3	5	9	8	4	11	3	4	11	3	9	6
48	—	—	1	3	2	5	5	3	4	7	2	7	—
49	—	1	—	—	—	—	—	1	1	3	—	1	2
50	—	1	—	—	—	—	—	—	—	2	—	—	—
51	—	—	—	1	—	—	—	—	—	1	—	—	—
52	1	—	—	—	—	—	—	—	—	—	—	—	—
	150	191	207	226	235	58	462	123	116	301	75	224	245

TABLE 13.

Humpback Whales: Group V.
Sexually immature in seasonal Catches
1949—1956.

EASTERN AUSTRALIAN COAST

Station	Year	Males			Females		
		Total	Immature		Total	Immature	
		No.	No.	%	No.	No.	%
Tangalooma	1952	448	26	5.80	150	28	18.67
	1953	509	21	4.13	191	40	20.94
	1954	420	30	7.14	178	46	25.84
	1955	429	21	4.90	171	31	18.12
	1956	407	22	5.41	193	32	16.58
Byron Bay	1954	91	4	4.40	29	2	6.90
	1955	65	4	6.15	55	6	10.91
	1956	78	1	1.28	42	3	7.14
All Eastern Australian Coast Stations	1952	448	26	5.80	150	28	18.67
	1953	509	21	4.13	191	40	20.94
	1954	511	34	6.65	207	48	23.19
	1955	494	25	5.06	226	37	16.37
	1956	485	23	4.74	235	35	14.89
Norfolk Island	1956	92	6	6.52	58	13	22.41
ANTARCTIC AREA V							
	1949/50	441	55	12.47	462	102	22.08
	1950/51	105	7	6.67	123	13	10.57
	1951/52	67	10	14.93	116	21	18.10
	1952/53	215	21	9.77	301	47	15.61
	1953/54	75	10	13.33	75	11	14.67
	1954/55	124	21	16.94	224	36	16.07
	1955/56	222	31	13.96	245	66	26.94

TABLE 14.

Frequency Distribution of Ovulation Counts from Female Humpback Whales in Catches at Tangalooma — Eastern Australia.

Year		1952	1953	1954	1955	1956
No. of pairs of ovaries examined		105	122	148	115	97
Ovulation counts. — % frequency distribution	0	13.3	15.6	25.7	18.3	17.5
	1— 3	31.4	32.8	37.2	32.2	16.5
	4— 6	21.0	19.7	12.8	14.8	28.9
	7— 9	12.4	15.6	9.5	13.9	20.6
	10—12	1.0	3.3	4.1	6.1	9.3
	13—15	1.9	5.7	4.7	6.1	4.1
	16—18	3.8	1.6	2.0	3.5	0
	> 18	15.2	5.7	4.1	5.2	3.1

TABLE 15.

Humpback Whales: Group V.
Females in advanced Pregnancy from seasonal Catches.

EASTERN AUSTRALIAN COAST

Station	Year	No. of mature females	Females in advanced pregnancy	
			No.	Percentage
Tangalooma	1952	122	8	6.6
	1953	151	11	7.3
	1954	132	19	14.4
	1955	140	*12	8.6
	1956	161	8	5.0
Byron Bay	1954	27	5	18.5
	1955	49	8	16.3
	1956	39	5	12.8
Total 1952—1956		821	76	9.3

* Including one case of twins.

ANTARCTIC AREA V

	1949/50	360	142	39.4
	1950/51	110	49	44.5
	1951/52	95	53	55.8
	1952/53	254	94	37.0
	1953/54	64	46	71.9
	1954/55	188	126	67.0
	1955/56	179	87	48.6
Total 1950—1956		1250	597	47.8

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Paper 12

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Apparent Variations in the Mean Length of Female Humpback Whales at Puberty

By

R. G. Chittleborough

Apparent Variations in the Mean Length of Female Humpback Whales at Puberty

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I. Introduction.

Catches of humpback whales taken at Australian whaling stations each year during the winter and early spring commonly include individuals which have just reached puberty. While puberal males can be distinguished only by histological examination of the testes, puberal females are readily identified from macroscopic examination of the ovaries. Since puberal females either have just ovulated, or are about to ovulate, for the first time, their ovaries contain a newly developed corpus luteum, a burst follicle, or a mature follicle exceeding 30 mm in diameter (Chittleborough 1955), with no corpora albicantia.

From 1949 to 1959, 313 puberal female humpback whales have been examined at Australian whaling stations. In this paper the lengths of these females are analysed and the results discussed.

II. Mean length of puberal female humpback whales.

a) Samples from the west coast of Australia.

Chittleborough (1955) found the mean length of puberal female humpbacks to be 38.50 ft. This estimate was obtained from a sample of 77 puberal females examined on the west coast of Australia between 1949 and 1954. During this period the numbers of puberal females obtained each year were barely adequate to enable the mean lengths to be compared from one year to another, but apparently the mean length of the puberal females varied very little during these years.

Chittleborough (1955) showed that the mean length at puberty of 38.50 ft. afforded a reliable method of calculating the percentage of immature females in a commercial catch during the period from 1949 to 1954. However, the application of this length to the catches of more recent years, gave results which were seldom consistent with the percentages of immature females as determined by examination of the ovaries (Chittleborough 1960, Table 8). Because of this it would appear that there had been some change during recent years in the mean length of females at puberty.

The mean lengths of the samples of puberal females taken on the west coast each year from 1956 to 1959 are shown in Table 1. In 1956, although the sample of puberal females was relatively small, the mean length was considerably greater than that of the sample accumulated from 1949 to 1954. Table 1 shows that since 1956 the mean length of the puberal females has decreased each year until in 1959 the mean was below that of those examined between 1949 and 1954.

Table 2 shows the results of comparisons of mean lengths of the samples shown in Table 1, using the «t» test. In 1956, 1957, and 1958 the mean lengths of the samples of puberal females from the west coast were significantly higher than that of the sample gathered from 1949 to 1954. Although there was a significant difference between the mean length of the sample from 1959 compared with that of 1958, the mean length of the former did not differ significantly (at the 5 % level) from that of the combined west coast sample from 1949 to 1954.

b) Samples from the east coast of Australia.

On the east coast the mean length of puberal females sampled from 1952 to 1954 varied insignifi-

Table 1.

Mean lengths of samples of puberal female humpback whales from Australian coasts.

Sample	No.	Range (ft)	Mean (ft)	S.D.	S.E.
West Coast					
1949—54	77	35.25—43.50	38.50	1.66	.18
1956	17	35.25—45.50	40.15	3.04	.74
1957	42	35.75—44.50	39.49	2.18	.34
1958	59	35.00—43.25	39.08	1.11	.14
1959	43	35.00—40.50	37.96	1.45	.22
East Coast					
1952—54	60	34.50—42.17	38.51	1.73	.22
1956—59	15	36.33—43.00	39.38	1.81	.47

Table 2.

Comparison of mean lengths of samples of puberal female humpback whales from Australian coasts by means of «t» test.

Samples compared	«t» value	Degrees of freedom	p.
West coast			
1949—54 vs 1956	3.245	92	<.01
1949—54 vs 1957	2.874	117	<.01
1949—54 vs 1958	2.415	134	.02> p> .01
1958 vs 1959	4.414	100	<.01
1949—54 vs 1959	1.869	118	.10> p> .05
East coast			
1952—54 vs 1956—59	1.736	73	.10> p> .05

cantly from year to year, the variations being well within those which might be expected in small samples taken at random from a population. Table 1 shows that the mean length of 60 puberal females taken on the east coast from 1952 to 1954 was practically the same as that of puberal females taken on the west coast from 1949 to 1954.

Since 1956 only small numbers of puberal females have been taken on the east coast of Australia. This has been due mainly to the shorter period of catching in recent years, quotas on that coast being filled by the beginning of August, compared with longer seasons extending to the end of September or the beginning of October in earlier years.

Table 1 shows that the mean length of puberal females taken on the east coast from 1956 to 1959 was greater than that of those taken in the same region from 1952 to 1954, but as shown in Table 2, the comparison of these mean lengths by the «t» test was inconclusive.

III. Discussion.

When considering the evidence available up to 1957, Chittleborough (1958b) suggested that linked with the decrease in numbers of whales in the Group IV (70°E.—130°E.) population, the younger whales were then growing more rapidly than in earlier years, resulting in an increase in the mean length at puberty during 1956 and 1957. The declining mean length of puberal females from the west coast each year from 1956 to 1959 shows that this theory was incorrect.

Figure 1 shows the graphical comparison of these samples of puberal females using the method of Hubbs and Hubbs (1953). The changes in these means can be related to known changes in methods of whaling operations in Australian waters during these years.

From 1949 to 1954 Australian whaling stations generally did not attempt particularly stringest selection of the largest whales, most individuals exceeding the minimum legal length (35 ft.) being

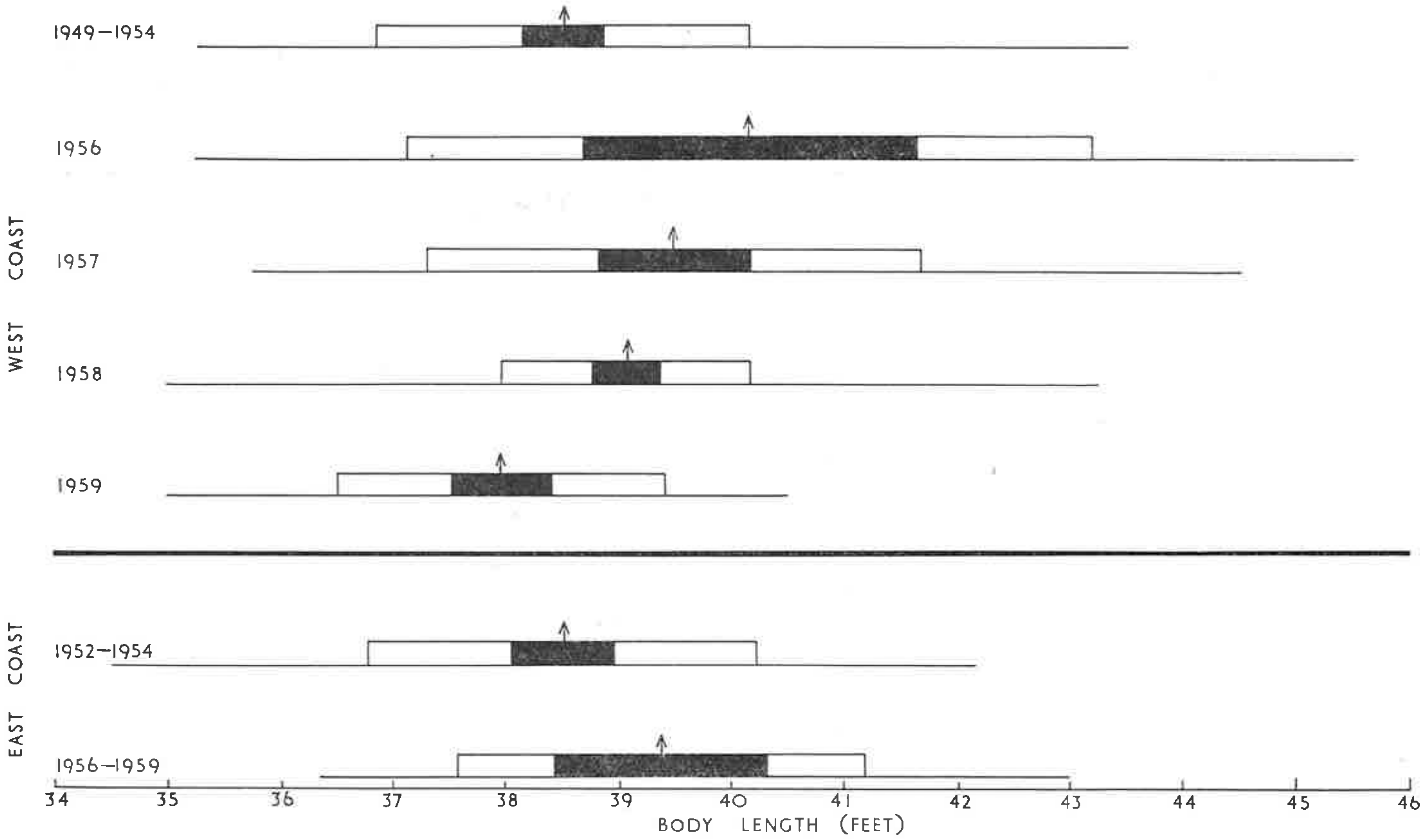

Fig. 1.— Comparison of body lengths of puberal female humpback whales in samples taken in various years in the west and east coasts of Australia. Heavy line shows observed range; arrow gives mean length; black bar extends 2 standard errors of the mean on either side of mean; hollow bar ends one standard deviation on either side of mean

exposed to hunting. During these years the mean length of puberal females was 38.5 ft. both on the west and east coasts of Australia.

In 1955 quotas of humpback whales allotted on the west coast of Australia were reduced, following evidence of some deterioration in the condition of that stock (Chittleborough 1958a). The reduction in quotas stimulated the whaling companies to encourage more careful selection by gunners of the larger whales. By more stringest selection the composition of the catch improved in 1955 and 1956, not only on the west coast but also on the east coast (Chittleborough 1958a).

On the west coast the higher degree of selection applied in 1956 resulted in a biased sample of puberal females, the relatively small number taken consisting mainly of the larger individuals. The mean length of puberal females taken on the west coast in 1956 was thus much higher than that of those sampled in earlier years.

Selection of large whales was continued after 1956, but on the west coast the decline in the size of that stock meant that selection was less successful each year (Chittleborough 1959, 1960). Thus more puberal females were taken in recent years and these were less restricted to the larger individuals with the result that the mean length of samples of puberal females decreased each year from 1956 to 1959 (Fig. 1). During this period considerable numbers of immature whales were taken (Chittleborough 1960). Since by selection the immature whales killed represented the larger individuals in the immature year classes, by 1959 the larger puberal females were under-represented in the catch. As a result the mean length of puberal females sampled on the west coast in 1959 was slightly less than the true mean length of puberal females in the original stock.

The effect of selection of large whales was also reflected to some extent in an apparent increase in the mean length of puberal females taken on the east coast of Australia from 1956 to 1959 (Fig. 1). However, the population which frequents the east coast is sufficiently large to enable quotas in recent years to be filled before many puberal females have been captured.

IV. Conclusions.

On the Australian coast, the mean length of puberal females varied with the degree of selection applied by gunners and was also influenced by the size of the stock remaining after intensive commercial operations.

Although none of the samples discussed in this report were completely random samples of puberal females taken from an undisturbed population, those taken between 1949 and 1954 are considered to be more representative than the samples obtained since 1954. The mean length of female humpback whales reaching puberty on the Australian coast is then very close to 38.50 ft.

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A/S HANDELSTRYKKERIET - SANDEFJORD

Paper 13

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TOPIC 1

EXPERIENCE PAPER: "LICENCE LIMITATION AS APPLIED TO WHALING"

-By R.G. Chittleborough

I. HISTORY OF CONTROLS

In its early history, whaling was not subject to limitation of either catch or effort and, as a result, the industry went through the same cycle of rise and fall as each new whaling area was discovered; catches rose as vessels increased in number, reached a peak and then declined despite high levels of effort. Records of catches are generally available for the era of sailing ships but the only measure of effort is an approximate estimate of the number of ships operating. In Arctic whaling, for example, probably 300-400 ships were operating in 1680 (the height of Dutch participation) and the average catch is reported to have been five to six whales per ship's cruise. One hundred years later (when British whalers had taken the leading position) apparently as many ships were whaling, but the catches had declined to two or three whales per ship (Ruud 1952).

Although the fishing power of these whaling ships was meagre in comparison with modern whaling fleets, the operations of large numbers of fishing units almost succeeded in eliminating the North Atlantic right whale (Balaena glacialis), the Greenland right whale (B. mysticetus), and the Southern right whale (B. australis). The sperm whale (Physeter macrocephalus) was less severely reduced, being saved by petroleum oil and its by-products which supplanted the markets of sperm oil. At the same time, the Australian gold rush drew crews from sperm whaling so that fewer ships were able to operate. The price of sperm oil dropped from 582 dollars per long ton in 1860 to 164 dollars in 1900.

Modern whaling, which began at the turn of the century with the introduction of harpoon gun, steam chaser, and floating factory ship, greatly increased the catching power of the fishing units. No limitation of catch or effort was applied until a dramatic increase in catch from 1928 to 1930 culminated in 1931 with the capture of 43,129 whales from which 3.7 million barrels of oil were produced.

Failure of the market for whale oil led to limitation of Antarctic catch from 1932/33, at first by voluntary agreements between whaling companies, and since 1937 by international agreements

The aim of the limitation was primarily to prevent a repetition of overproduction of oil, rather than conservation of individual species of whales or economy of fishing effort. Catch was expressed in terms of blue whale units, on the experience that a blue whale yields approximately the same amount of oil as two fin whales, or 2½ humpbacks or 6 sei whales (Ruud 1956). A delayed opening date for the Antarctic whaling season restricted the fishing effort somewhat, but the purpose of the delay was to ensure that the whales were able to feed and fatten after returning from the breeding grounds in lower latitudes.

The catch limit (in blue whale units) applied to the whole of the Antarctic region did nothing to encourage economy of effort. On the contrary, more catching vessels of greater fishing power were attached to each factory ship, each expedition endeavouring to take the highest possible proportion of the total catch permitted. An early attempt to restrict the number of fishing units was included in the bilateral agreement between England and Norway for the season 1936/37 in which the numbers of catching vessels to each expedition were limited to 5, 6, or 7 according to tonnage and production capacity of the factories. However, in the same season, one German and two Japanese expeditions operated without restrictions.

In recent years, the countries engaged in pelagic whaling in Antarctic waters have negotiated to divide the overall catch limit between themselves in a step towards more national use of the resources.

The restriction of catch in terms of blue whale units had no foundation of sound conservational practice, since it ignored the fact that several species differing in abundance were represented in the catch. The history of whaling records many instances where individual species have been reduced to the verge of extinction because the industry has been sustained by the simultaneous exploitation of more numerous species. For example, the presence of larger stocks of fin whales enabled pelagic operations in the Antarctic during postwar years to be continued on blue whales long after this species would not itself sustain commercial operations.

In recent years the rate of exploitation of blue and humpback whales has been separately regulated in Antarctic whaling by specific provisions concerning dates of open season. In the case of humpback whales, an overall Antarctic catch limit of 1250 humpbacks was applied each summer from 1949/50 to that of 1951/52, and thereafter the catch was limited by the brevity of the open season (generally of four days only). The fact that that there were five separate stocks of humpback whales, differing in initial size and history of exploitation, was largely ignored, as was the fact that some of these stocks were being hunted simultaneously in lower latitudes.

When postwar whaling began in Australian coastal waters, the Government allotted separate quotas of humpback whales to each whaling company. This method of catch limitation had the obvious advantage that each company could set its fishing effort at an economic level instead of competing against other companies to secure the highest proportion of an overall limit. Competition between companies was then for the highest efficiency of oil extraction.

No information is available indicating the basis upon which these quotas were originally selected, but in the light of subsequent events (Chittleborough 1963) there can be no doubt that the quotas were too large, even if there had been no fishing upon these populations in Antarctic waters.

II. THE MEASUREMENT AND USE OF EFFORT STATISTICS IN WHALING

1. The Nature of Fishing Power, Fishing Effort, and Catchability in Whaling.

A considerable, and obvious, difference lies between the operations of whaling and those of fishing with trawls and gill nets. The appearance of whales at the surface, in areas they are known to frequent, and the manner of killing them, make each whaling operation more purposively directed to its objective than the dragging of a trawl over the sea-floor to gather fish from a guessed-at density in a distribution assumed from past experience. As a basis to discussion, let us assume that the fishing power of a catcher is represented by the ratio of the area it can search effectively in a unit time (say, one hour) to the total area occupied by the stock being fished, and that the catchability of a single whale (its vulnerability) in that area in that interval is a function of (1) its risk of being contacted (seen) by the catcher, (2) its risk of being approached close enough, by the catcher, for the harpoon to be fired and for the harpooner to make a hit. The converse of each of these probabilities, from the whale's viewpoint, is:

(1) its chance of being submerged at all times that observers on the chasers look in its direction, (2) its chance of outpacing the catcher and of diving to avoid the fired harpoon and of changing direction successfully underwater.

Measurement of these quantities may be approached *a priori, a posteriori* and by a combination of these. Thus, through the *a priori* approach we may estimate fishing power by measuring the speed at which a vessel can move in searching and we may measure the span, from one side of the ship to the other, over which its observers can reliably search; we also may refine these measures by allowing for differences in sea conditions which affect the speed of movement and visibility. In attempting an estimate of catchability we would make use of information on the behaviour of the whales in alternately surfacing and submerging, and of estimates of the probability of contact at various levels of density. *A priori* estimate of a catcher's chances of making a capture after having made a contact is unlikely to be possible, although the means of increasing such chances (e.g. increased manoeuvrability) could be identified. An *a posteriori* approach to this matter will take some data of fishing operations, such as days of operation, hours of steaming or hours of hunting, and will arrive at estimates of catchability by reference to estimates of stock density and of total and fishing instantaneous mortality. If unadjusted operational data are used for this purpose, some of the effects of factors which influence catchability will be included in the measure of what is here defined as fishing power. A combination of the two methods circumvents some of the practical difficulty of the *a priori* approach and increases the rigour of the *a posteriori* approach.

2. Measurement of Effort in Humpback Whaling

The unit of effort used in earlier whale research was the *catcher's day's work*, introduced by Hjort, Lie and Ruud (1933). This unit should refer only to hunting days: days lost by individual catchers due to adverse weather, mechanical failure, etc. should not be included as fishing effort. Hjort, Lie and Ruud were well aware that the catcher's day's work was not of constant value, but at that time they considered that the variability of this unit was of minor importance in comparison with changes in the size of the stock. However, subsequent events showed that in using this measure of effort for stock assessment purposes some of its variability had to be removed.

The importance of some of the variable elements of this unit can be demonstrated from data obtained in recent years from whaling operations along Australian coasts.

Strictly speaking the unit was a catcher's working day and that which was recorded was simply the number of days on which each catcher did any work. However, the proportion of each such working day spent in actual whale hunting varies for three different sets of reasons: 1) capacity of processing plant, 2) weather conditions, 3) incidental effects.

In the earlier years of operation of the Australian whaling stations, the daily catching power of the vessels was generally greater than the daily processing capacity of the factory. Because of this, catching vessels were very often allotted a fixed number of humpback whales to be killed in a day. In successive years the average catch per catcher's day's work increased (Figure 5) because whales were processed more rapidly as a result of improvements in factory capacity and efficiency. But this increase in catch per day was obtained by increased expenditure of effort.

The number of hours per day spent in whaling during a season at one locality can vary inversely to changes in density of whales passing that point. For example, at Tangalooma in 1960, there was a mean of 10.35 hunting hours per catcher day from June 6 to 15; a mean of 7.95 hunting hours per catcher day from July 6 to 15 (height of migration past this station); and a mean of 10.68 hunting hours per catcher day from August 6 to 15 (end of northward migration). Presumably these differences derive largely from limits set by plant capacity.

The number of hours spent in whaling during each catcher day may vary from one station to another (during the same year). For example, throughout the 1959 season the catcher at Byron Bay maintained an average of 8.8 hours of steaming per day, while in the same year, catchers at Carnarvon averaged 12.7 hours of steaming per day. At the same time, catchers operating on these populations of humpback whales in Antarctic Areas IV and V were presumably steaming (and hunting) for almost the whole of each 24 hours because of the prolonged period of daylight.

The hours spent hunting in a particular day may be reduced because of adverse weather, yet in the original definition of this unit of effort, such a day is rated as of equivalent fishing effort as a day when a catcher could stay on the whaling grounds throughout daylight hours. This effect of weather upon the hours spent whaling might be expected to occur at random, so that it might not be important when comparing rates of catching over long periods of time. However, whalers themselves have claimed that adverse weather conditions have affected the success of their operations and while their claims that this effect had been the real cause of the appearance that the density of whales fell from one year to another (Chittleborough 1960) could not be accepted, their evidence on this effect of weather is important in this work.

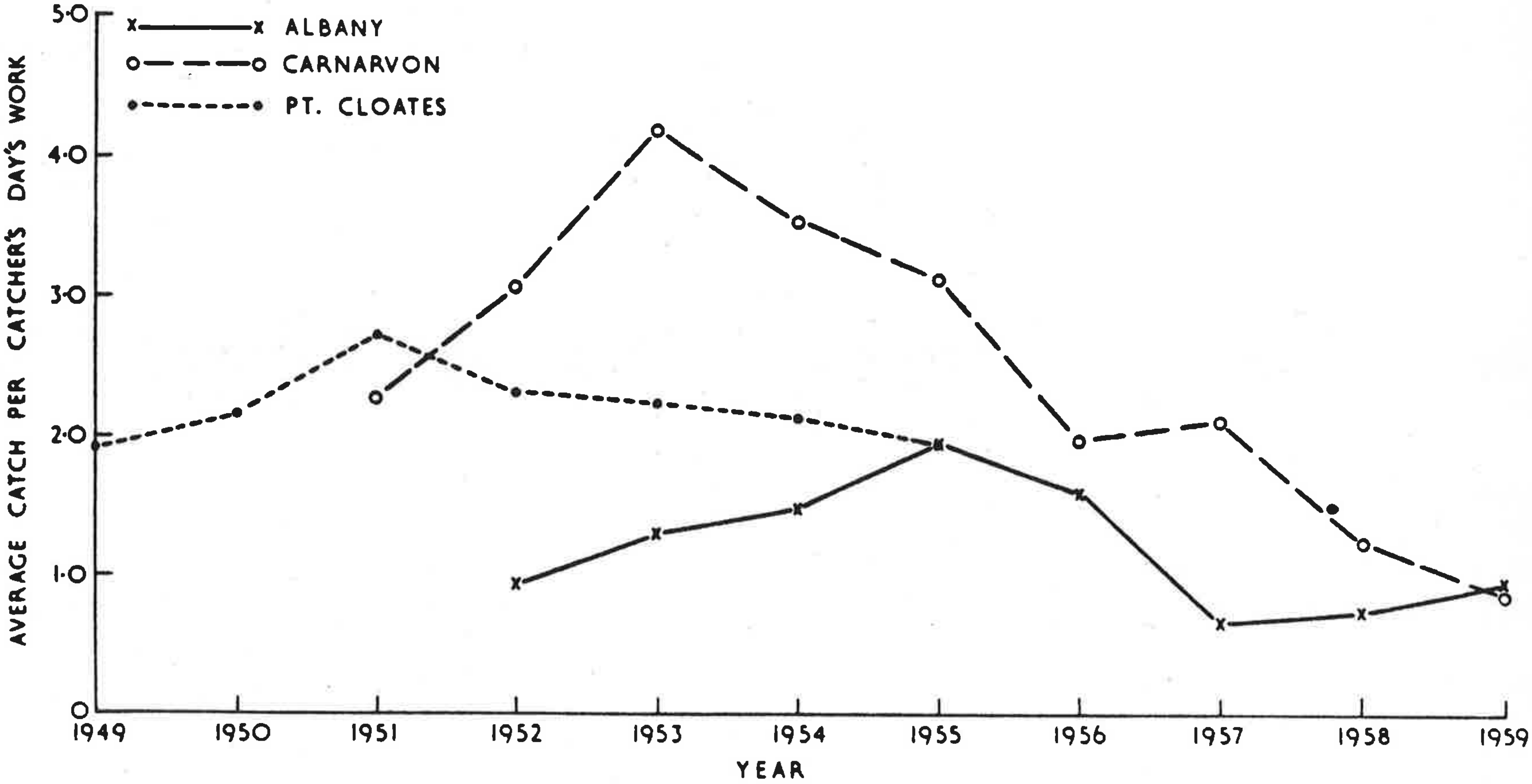

FIG. 5. AVERAGE ANNUAL CATCH (HUMPBACKS) PER CATCHER'S DAY'S WORK AT SHORE STATIONS ON THE WEST COAST OF AUSTRALIA. (FIG. 21 OF REVISED MANUSCRIPT OF POPULATION PAPER.)

The examples given above show that the catcher day cannot be a constant unit of time. In an attempt to obtain a more precise unit in terms of which to measure fishing effort and one which would more closely conform to the idea of fishing power given above, all available ships' logs from Australian whaling companies were examined. Where a log had been kept in detail, the different operations of each day, and the time devoted to them, could be assigned to various categories, viz:

(a) Total steaming time. All the time absent from moorings, irrespective of duties.

(b) Steaming time of each day's whaling. This excludes time spent away from moorings when engaged in bunkering, victualling, moving whales moored from the previous day's catch, and other transport duties.

(c) Steaming time hunting (and killing) whales. This excludes time spent steaming out to whaling grounds from the previous night's anchorage, and also excludes time spent towing whales back to the station (and returning to the whaling grounds). Obviously hunting is restricted to daylight hours, whereas (b) may include several hours of darkness.

The Catcher's steaming hour, category (b), is a more precise measure of whaling effort than the catcher's day's work, since time at anchor (when the factory does not require more whales) is omitted. This unit also omits parts of days lost because of minor repairs, refuelling, adverse weather, etc. Hours spent towing the catch back to the station are included in this unit of effort, which would not matter if it were a constant element. However, the number of whales that some catchers can tow is smaller than that which other catchers can tow and their towing speed is lower. Consequently, even though they may be as effective as other vessels in hunting, these slower towing vessels lose time and in a given period of steaming time would spend a smaller proportion in actual hunting. Their catch per hour's steaming would be lower. Again a catcher's steaming hour at Tangalooma was not the same as a catcher's steaming hour at other stations, because at Tangalooma one of the whaling vessels was stationed on the whaling grounds each day to act solely as a towing vessel. Thus although the catching vessels might tow some whales to the station, their steaming time included a much lower proportion of towing time than did the steaming time of catchers at other stations.

The Catcher's hunting hour, (category (c) above) is in theory the most precise measure of whaling effort, since it measures only that effort which directly determines the capture of whales. However, many ships' logs carried insufficient detail to permit identification of hunting time in each day's operations. Thus, the catcher's steaming hours have been used as measure of the effort expended by vessels operating at Point Cloates, Carnarvon, and Albany. At Tangalooma and Byron Bay, however, catchers' hunting hours could be assessed.

The effective effort of the catcher's day has also been increased by mooring the catchers closer to the whaling grounds, and by the use of spotting aircraft. The increased effort achieved by these means has been calculated in terms of catcher hours (Chittleborough 1962).

In the conversion of aircraft flying hours into equivalent catcher hour units, 1 aircraft flying hour was shown to be equal to about 5 catcher steaming hours. This relation was calculated where sighting records were made simultaneously from catchers and aircraft operating in the same area at the same time. For example, off Albany in the winter of 1961, two catchers sighted 226 humpback whales in a total of 605 steaming hours; that is, 2.68 hours of steaming were required to sight one humpback whale. In the same period, the spotting aircraft sighted 241 humpback whales in 144.6 flying hours, i.e. 0.60 flying hours for each humpback sighted. In this instance, 2.68 catcher steaming hours were equivalent to 0.60 aircraft flying hours, or 4.7 catcher steaming hours were equivalent to 1 flying hour.

The relation between the catcher's steaming hour and the aircraft's flying hour would no doubt vary for different aircraft, catchers, personnel, and localities, but where the ratio could be calculated, the result was close to the value of 5 catcher steaming hours = 1 aircraft flying hour and this ratio has been used in calibrating fishing effort.

The physical basis of this ratio is thought to be as follows. The aircraft travels at about 10 times the speed of the catchers; experience has shown that an observer in an aircraft can effectively scan about the same width of water as an observer on a ship. However, the aircraft searching is apparently half as effective as ship searching, presumably because of the relation between aircraft speed and the rhythm of whale exposure at the surface. Thus, the aircraft's 10 times greater search area is reduced to 5 times.

In the measurement of fishing effort, variations in the "catching power" of whaling vessels present more difficulties than the units of time. The Australian whaling industry has employed as wide a range of types of vessels for hunting whales as could be found engaged in whaling in most other countries. Vessels differed very greatly in size, age, speed, manoeuverability, towing power, and ability to operate successfully in heavy seas. Two small, speedy launches, working together as one unit in coastal whaling, and the large, steel "Antarctic" type chaser, were not equivalent fishing units, nor would efficiency of one type have maintained the same relation to the other under varied operating conditions (such as weather, or configuration of the coastline).

Table 7 shows that similar vessels, operated in the same locality, at the same time, by gunners of similar experience, achieved similar rates of catching. When dissimilar vessels, operating in one locality at the same time, are compared (Figure 6), their contrasting rates of catching reflect their various efficiencies, during a period when whales were plentiful. However, when the population had been depleted, rates of catching converged upon a single low level, indicating that differences in catching power were less important when whales were scarce. That is, a capture in any interval of time was a chance event whose probability was about equal for each catcher and was so small as to be only little affected by differences of area searched.

Some catchers have operated in all of the past seasons on their part of the Australian coast. This simplifies the analysis of fishing effort, because, as pointed out by Hjort, Lie and Ruud (1933), operations by the same vessels can be compared directly from one season to another. For present purposes, four catchers which hunted every year on the west coast, and two which hunted every year on the east coast, have been used as standard units of catching power. The steaming or hunting hours of these catchers working in the same localities each year, and over the same period of time (during the northward migration) have been assessed. Adjustments have been made to the effort in these years where the effective hours were increased by the introduction of spotting aircraft or a change of moorings. These adjustments have been made in terms of equivalent steaming or hunting hours by the catchers used as the standard.

TABLE 7

OPERATIONS OF CATCHERS AT TANGALOOMA DURING PERIOD JUNE 10 TO AUGUST 5 OF EACH SEASON - 1953-1962

Year	Vessel	Total days hunting	Total hours hunting	Total hump-backs killed	Average hunting hours per day	Average whales per catcher's day's work	Average whales per hunt-ing hour	Average hours per whale
1953	Kos I	55	247	171	4.49	3.11	0.69	1.44
1954	Kos VII	50	291½	157	5.83	3.14	0.54	1.86
1955	Kos II	45	312½	234	6.94	5.20	0.75	1.34
	Kos VII	56	326	263	5.82	4.70	0.81	1.24
	Total	101	638½	497	6.32	4.92	0.78	1.28
1956	Kos II	55	367	265	6.67	4.82	0.72	1.38
	Kos VII	55	374	257	6.80	4.67	0.69	1.46
	Total	110	741	522	6.74	4.75	0.70	1.42
1957	Kos I	55	387½	270	7.05	4.91	0.70	1.44
	Kos II	55	373½	274	6.79	4.98	0.73	1.36
	Total	110	761	544	6.92	4.95	0.71	1.40
1958	Kos I	55	389½	291	7.08	5.29	0.75	1.34
	Kos II	54	298½	300	7.38	5.56	0.75	1.33
	Total	109	788	591	7.23	5.42	0.75	1.33
1959	Kos I	57	401½	302	7.04	5.30	0.75	1.33
	Kos II	57	418	305	7.33	5.35	0.73	1.37
	Total	114	819½	607	7.19	5.32	0.74	1.35
1960	Kos I	57	532½	270	9.34	4.74	0.51	1.97
	Kos II	57	528½	284	9.27	4.98	0.54	1.86
	Total	114	1061	554	9.31	4.86	0.52	1.92
1961	Kos I	56	534¾	119	9.55	2.13	0.22	4.49
	Kos II	57	550½	131	9.66	2.30	0.24	4.20
	Total	113	1085¼	250	9.60	2.21	0.23	4.34
1962	Looma II	47	488¾	38	10.40	0.81	0.08	12.86
	Looma III	47	500	30	10.64	0.64	0.06	16.67
	Total	94	988¾	68	10.52	0.72	0.07	14.54

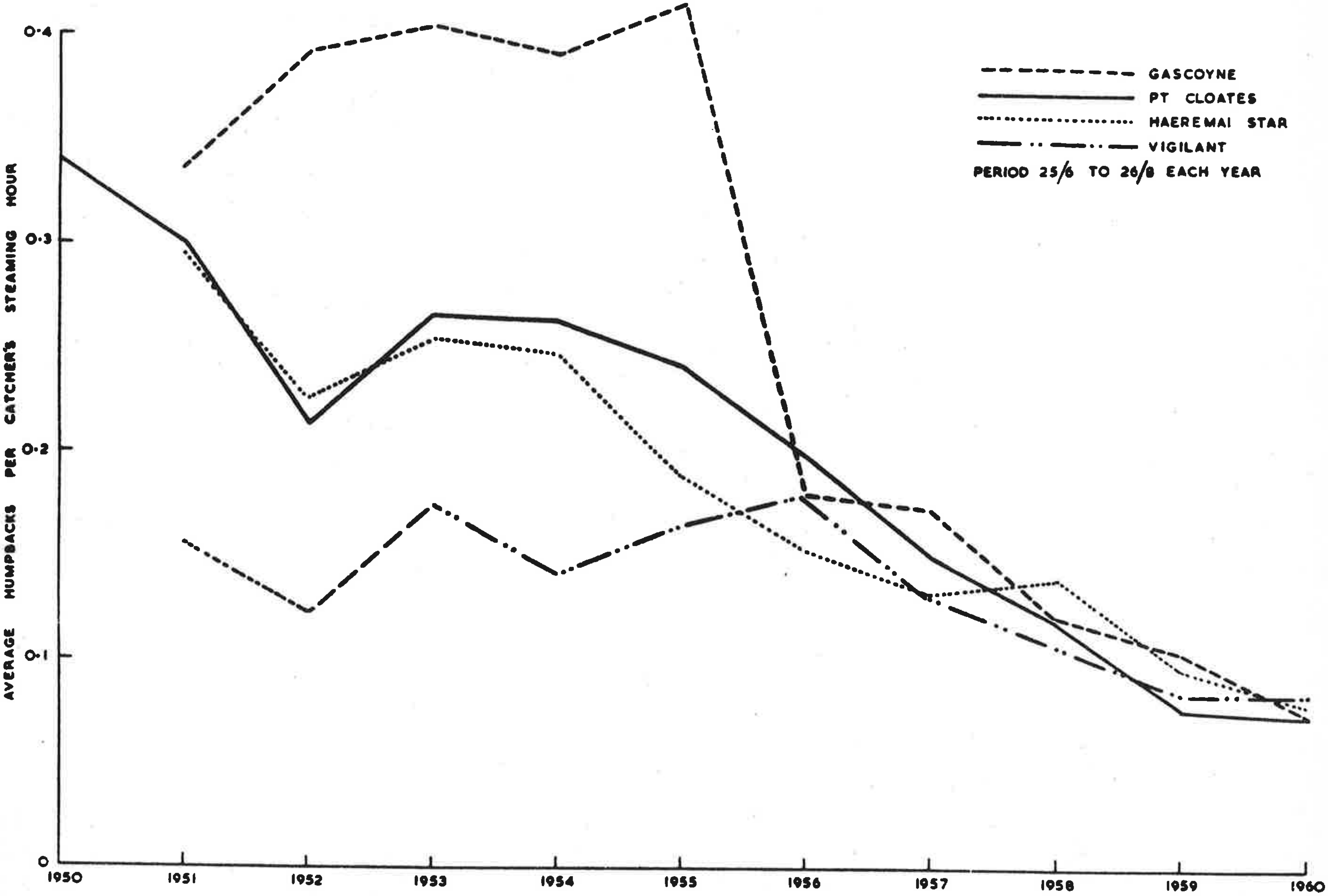

FIG. 6. CATCH PER UNIT EFFORT BY FOUR CATCHERS OPERATING ON THE WEST COAST OF AUSTRALIA DURING THE SAME PERIOD EACH YEAR. (FIG. 22 OF REVISED MANUSCRIPT OF POPULATION PAPER.)

The unit of effort used for the Australian seasons prior to 1955 was not precisely the same as that from 1955 onwards. Owing to a reduction in quota, a more vigorous management policy made the unit fishing time more effective from 1955. The mortality coefficient of 1954-55 can be taken to have been the mean of the 1953-54 and the 1955-56 mortalities, and if this were so then the effort units in 1954 and earlier years have to be reduced by a factor of 0.7 to equate them with the effort units of 1955 and later years.

3. Use of Effort Statistics in Assessment of Humpback Stocks

In the preceding section, a demonstration has been given of the intrinsic and misleading variability of catcher's working day as a unit of effort. If this unit of effort had been taken to be constant in the early years of Australian operations (Figure 5) the increase in catch per day would have been interpreted as representing an increase in availability of whales.

On the other hand, use of the catcher day as a unit of effort can mask a decrease in the availability of whales. For example, Table 7 shows that at Tangalooma in 1960, the catch per catcher's day's work was only slightly less than in previous years, but considerably more hours were spent hunting each day in 1960 than in previous years. In other words, a greater effort had to be expended each day in 1960 in order to maintain a daily rate of catching similar to that in previous years.

From the adjusted effort, in standard units, applied by the same catchers operating in the same locality over the same period of time, and the catch of humpback whales taken by these same vessels under those conditions, indices of relative abundance (catch per unit effort) have been calculated for each year (Table 8).

When using the catch per unit effort to compare the abundance of whales from one year to another, the calculations had to be made with respect to the same period of each year because, as shown by Chittleborough (1962), the abundance of whales changes during the season, as the northward and southward migrating streams pass each shore station. The opening date and length of season has fluctuated at each Australian whaling station, but in most cases the stations were operated throughout the greater part of the northward migration.

TABLE 8

ADJUSTED EFFORT, HUMPBACK CATCH, AND CATCH PER UNIT EFFORT, BY CATCHERS ADOPTED AS STANDARD FOR OPERATIONS ON GROUP IV AND V POPULATIONS

	Standard Catchers* from Group IV Population			Standard Catchers** from Group V Population		
Year	Adjusted Effort (Steaming hours)	Humpback catch (No.)	Catch per unit Effort	Adjusted Effort (Hunting hours)	Humpback catch (No.)	Catch per unit Effort
1950	341	162	.475	-	-	-
1951	995	422	.424	-	-	-
1952	1568	544	.347	-	-	-
1953	1465	517	.353	176	171	.972
1954	1852	650	.351	208	157	.755
1955	2378	580	.244	638	497	.779
1956	2631	467	.178	741	522	.704
1957	3351	489	.146	761	544	.714
1958	2847	350	.123	788	591	.750
1959	3015	271	.090	820	607	.740
1960	3957	245	.062	1061	554	.522
1961	6557	358	.055	1085	250	.230
1962	5524	284	.051	989	68	.069

* The same four catchers operating on the west coast of Australia from June 25 to August 26 each year.

** Two catchers operating on the east coast of Australia from June 10 to August 5 each year.

At Carnarvon, the relative abundance (catch per unit effort) of humpbacks was measured each year from June 25 to August 26 (this being the only period when catching was in progress in every year from 1951 to 1962). At Tangalooma, the relative abundance of humpbacks was measured each year from June 10 to August 5.

Estimates of the total annual effort on the west coast of Australia were obtained for each winter season by multiplying the adjusted effort of the standard west coast catchers by the ratio of the total west coast catch to the catch by the standard catchers. The Antarctic (Area IV) effort was estimated by dividing the catch in each summer by the mean catch per unit effort of the standard west coast catchers during the two adjacent winters. Corresponding estimates of total annual effort exerted to take the catches from the Group V population were made using the data from the catchers taken as standard on the east coast of Australia.

Humpback fishing effort in Antarctic Areas IV and V had to be estimated in terms of the Australian units, partly because full details of the effort data were not available from these areas, and also because a variety of species was being hunted simultaneously in these southern feeding grounds, making it extremely difficult to separate from the overall Antarctic effort, that portion which had been applied to humpback whales.

III. CATCH AND LICENCE LIMITATION

As already discussed, attempts to conserve humpback whales by means of catch and licence limitation were unsuccessful, partly because each unit stock was not given separate consideration, and also because of a lack of information upon stock size and sustainable yields. The Groups IV and V (west and east coasts of Australia) breeding stocks of humpbacks have each been reduced to a few hundreds. In July 1963, the International Whaling Commission passed a resolution prohibiting the capture of humpback whales in the southern hemisphere.

The maximum sustainable catch from the Group IV population (70°E.-130°E.) would probably be taken from a stock containing 10,000 humpback whales (which was about the level in 1949). The best estimate of the period of protection needed for the remnants of this population to recover to that level is 49 years, the most optimistic estimate (using the highest possible value for r, and a very low value for M) is 28 years. The maximum sustainable yield if the population were allowed to recover, has been estimated to be 390 humpbacks per year (Chittleborough, 1963).

Corresponding estimates for the Group V population (130°E. - 170°W.) are that the maximum sustainable catch of 330 humpback whales could be taken from a stock level of 8,500 humpbacks after a recovery period of more than 36 years (best estimate 63 years)

The maximum sustainable catches from these populations are so low that at most each population might support one modest shore station or two small stations. The effort required to take the maximum sustainable catch each year can be estimated from the data gathered during recent whaling operations.

Chittleborough (1963) calculated that the average catching power of the four catching vessels adopted as a standard for the Group IV population was 0.1 humpbacks per catcher steaming hour for every 2,000 humpback whales in the catchable stock. When the Group IV population has recovered to the level where the maximum sustainable catch can be taken (catchable stock 10,000 humpbacks) the standard catchers could average 0.5 humpbacks per steaming hour. Thus the sustainable catch of 390 humpbacks would require the expenditure of a total effort of 780 steaming hours. If a catcher steamed for thirteen hours per day, the total catch of 390 whales would be taken in 60 whaling days at a rate of 6.5 per day. This rate is somewhat above the average towing capacity of the catchers used as the standard. Therefore two catchers would be required or one catcher could be operated over a longer period but steaming fewer hours per day. Two catchers, each steaming 6.5 hours per day, and each taking 3.25 humpback whales per day, would take the sustainable catch of 390 humpback in 60 days (assuming no delays due to weather). These estimates are based on operations on the west coast of Australia during the northward migration. Operating costs would no doubt determine the number of catching vessels to be used in order to maximise the net economic gain from a catch limit based on maximum sustainable yields.

The foregoing forecast is, of course, of the operation of catchers similar to those from whose operations are represented in the data from which the forecast was made. Over the indicated time spaces (28 to 63 years) for recovery, significant changes are likely to take place in whaling equipment. An *a priori* approach to the vessels of the future, taking advantage of results such as those referred to here, should provide a sound basis for decisions to be made at that time.

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Paper 14

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DYNAMICS OF TWO POPULATIONS OF THE HUMPBACK WHALE, *MEGAPTERA NOVAEANGLIAE* (BOROWSKI)

By R. G. Chittleborough

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CONTENTS

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Summary

Results of studies of the structure and dynamics of two humpback whale stocks of the southern hemisphere (group IV, 70°E.–130°E.; group V, 130°E.–170°W.) are drawn together. Estimates are made of recruitment and mortality rates, and an assessment is made of the yields to be taken from these stocks under various conditions.

The two stocks are shown to be, in the main, independent of one another although there is a negligible sporadic exchange between them. The group V stock is shown to fragment, but probably randomly, in its northern migration.

Reproduction, nutrition, and growth are described. Birth rate of females is estimated to be 0·186, and since the sex ratio is approximately 1, the total birth rate is about 0·37. Parameters (von Bertalanffy) for growth are L_∞ 42·58 ft for males, 45·21 ft for females; $k♂ = 0{\cdot}266$, $k♀ = 0{\cdot}205$.

The history of exploitation is reported.

Population structure is described from evidence drawn from examination of commercial catches; substantial changes in recent years (reduction of the numbers in older groups) are described.

Measurement of effort, and an analysis of variations in selectivity of the killings are reported in detail.

Decline in the abundance of these groups, group IV steadily since 1954 and group V sharply since 1959, is described.

Total mortality, natural mortality, fishing mortality, and recruitment rates are estimated and are used in estimating stock numbers and sustainable yields. The group IV stock probably consisted of 12,000–17,000 individuals in its unfished state, of about 10,000 individuals in 1949, and no more than 800 in 1962. The group V stock probably contained about 10,000 individuals in its unfished state, but only 500 or less in 1962. In its present state, group IV could give a sustainable yield of 18 (range 4–32) whales, and group V of 12 (range 3–21) whales. The maximum yields these stocks could sustain in completely regenerated state are: group IV, 390 whales per year; group V, 330 whales per year. Group IV would require 28–49 years to reach that state, group V would require 36–63 years.

I. INTRODUCTION

(*a*) *Objectives*

When postwar whaling was re-opened on the Australian coast, in 1949 on the west coast, and in 1952 on the east coast, a programme of research was commenced upon the two populations of humpback whales being fished. While the ultimate objectives of this research were the estimation of population size and assessment of maximum yields under various exploitation regimes, the parameters of the populations first had to be determined. Information concerning some of these parameters, i.e. migration, reproduction, age, growth, and population structure, has already appeared in various publications to which reference will be made in the relevant sections.

The present paper brings together all the available data (both published and unpublished) relating to these two populations, to measure the parameters more precisely, and to assess stock sizes and maximum yields at various levels of fishing.

(*b*) *Material*

(i) *Commercial Catches*

Apart from a few specimens killed under special licence for research purposes, material for the study of these populations has been obtained from humpback whales killed during commercial whaling operations. These operations were centred around shore-based whaling stations at Point Cloates, Carnarvon, and Albany on the west coast, at Tangalooma (Moreton I.), and Byron Bay on the east coast of Australia, at Norfolk I., and in Cook Strait, N.Z., the locality of each station being shown in Figure 1. Catches of humpback whales were also taken by whaling fleets operating in Antarctic waters to the south of Australia and New Zealand.

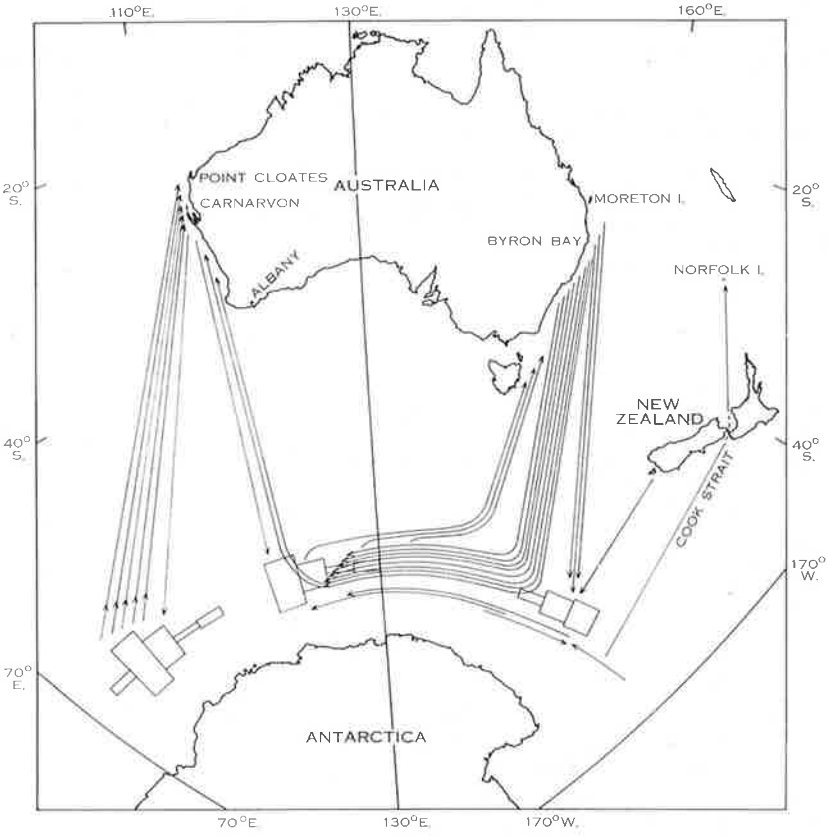

Fig. 1.—Individual movements (simplified) by 27 marked whales whose recapture provided evidence of migrating behaviour in 1958–59. Rectangles indicate location of Antarctic humpback whale catch in February 1959.

Commercial catches of whales are seldom (if ever) random samples of the populations from which they were drawn; in this case the following factors were of importance in the relationship between the commercial catch and the population.

The minimum legal length (35 ft) renders the young whales invulnerable to commercial operations. This regulation does not impose a knife-edge selection of the whales to be killed. Varying degrees of selectivity are applied by individual gunners. The level of selection may vary with the abundance of whales. When whales are plentiful, individuals of approximately 36 or 37 ft may be approached but passed by in favour of larger specimens.

The method and level of catch limitation may influence the degree of selection applied by gunners. In waters south of 40°S., where an overall catch limit has been applied, the competition for catch in the short season permitted has left little time for discriminating between whales, with the result that there has been very little selection of large whales. Each expedition has competed for the greatest proportion of the total limit. The allocation of separate quotas to each Australian station reduced the competition between these stations so that they could afford to be selective. Gunners were encouraged to take large whales so that the highest possible yield of oil could be obtained from the allotted quota. In some instances, gunners were offered bonus payments based on the lengths of the whales killed. On occasion, gunners have been instructed to take (where possible) only whales exceeding 40 ft in length. The allocation of separate quotas to each Australian station led to some competition between stations for the highest average oil yield per whale killed.

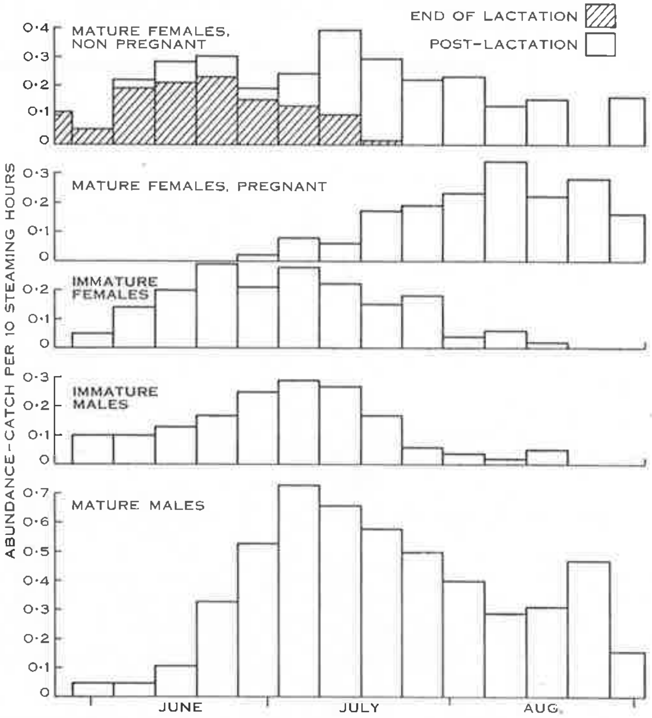

Fig. 2.—Abundance (at weekly intervals) of various categories of humpback whales during northward migration past Albany (35°05′S.).

A change in the quota can result in a change in the level of selection; for example, a reduction in the quota is likely to lead to the average size of the catch being somewhat higher than it would have been if the quota had remained unchanged, provided there are sufficient whales from which to select.

The protection of female whales accompanied by calves imposes another type of selection, a considerable proportion of the mature females being invulnerable at most times since lactation continues for nearly 11 months. Calves are weaned in June and early July (Chittleborough 1958*c*), such females and their "yearling" offspring being amongst the first to reach the Australian coast during the northward migration (Fig. 2). Although there is little doubt that the " yearling" offspring could survive even if its parent was killed just prior to, or during weaning, interpretation of the regulation protecting lactating females has varied from station to station and from year to year. At some stations, gunners have spared females accompanied by yearlings, or have taken these females only when no other whales could be found. Lactating females would then be absent, or under-represented in the commercial catch.

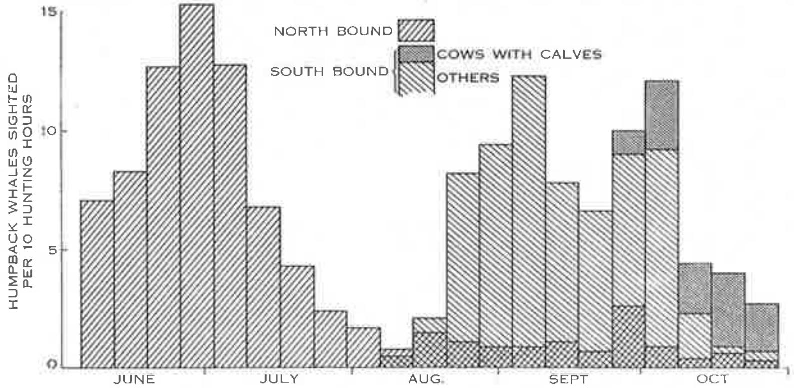

Fig. 3.—Average weekly density (sightings per unit effort) of humpback whales migrating north and south on the east coast of Australia in the vicinity of 28 °S. latitude during 1961.

At Australian whaling stations the availability of whales changes as the migrating stream passes during the northward and southward migrations (Figs. 3 and 4). Within the migrating stream there is some segregation of the various categories of humpback whales (Fig. 2). The period of commercial operations is then of importance to the question of whether the commercial catch samples the population fully. A whaling station with a small quota might fill its quota rapidly by operating only during the height of the migration past that station, and in consequence the beginning and end of the migrating stream might not be sampled.

On the other hand, an increase in the quota could extend the season so that a much more intensive effort would be required in order to locate sufficient whales. The station in Cook Strait, N.Z., has not been limited by a quota, and operated throughout the period of (northward) migration every year, so that its catch could be expected to have been more representative of the accessible population than the catches taken by stations operating under more restrictive conditions.

Commercial catches may vary in composition from one locality to another. For example, during the northward migration, pregnant females are carrying near-term foetuses, and the majority give birth soon after reaching the vicinity of 35 °S. Thus the catches at the more southerly stations, such as that at Albany, Western Australia, and at Cook Strait, N.Z., include high proportions of pregnant females in their catches. By the time these females pass the more northerly whaling stations, most are lactating and are, therefore, protected.

Since all factory ships and shore stations are required to send details of their catches to the Bureau of International Whaling Statistics, the records of humpback whales taken from these populations in recent years should be complete. However, there is evidence that not all catches of humpback whales taken in recent years have been reported to International Whaling Statistics.

During the summer of 1954–55, the factory ship *Olympic Challenger* apparently slaughtered humpback whales in the Antarctic without regard for the time of open season, or the minimum legal length. The Panamanian whaling inspectors on board attempted to cover these infringements by submitting falsified statistics of catches to the Bureau of International Whaling Statistics (Ruud 1956). In all, 1097 humpback whales were taken from the group V population, but 170 were reported to International Whaling Statistics, and 28 were taken from the group IV population although none was reported. These illegal catches are included in the total catches listed in Tables 1 and 2. There are grounds, reported later, for believing the records to be incomplete in other respects.

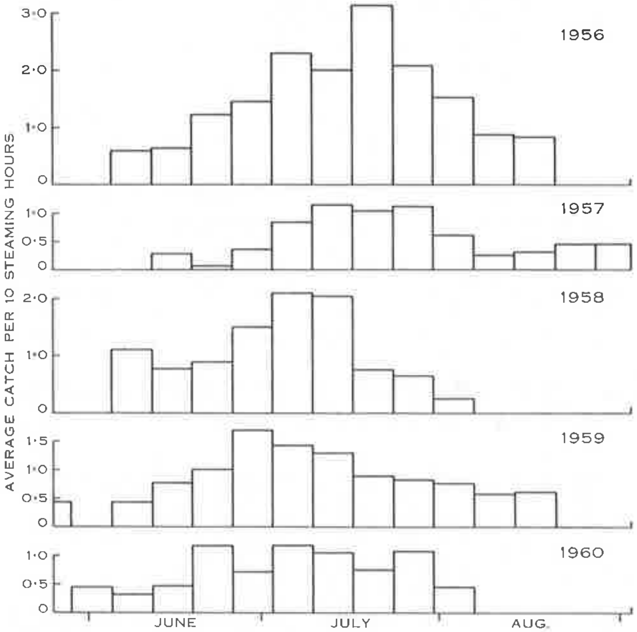

Fig. 4.—Relative abundance (catch per unit effort) of catchable humpback whales each week off Albany (35 °S.); northbound migration.

(ii) *Sampling of Catch*

Whaling inspectors on each shore station and Antarctic factory ship are required to record, with respect to each whale in the catch, the date and location of killing, the sex and total length, and in the case of females, the presence or absence of milk, and the sex and length of foetuses. These data are available for all humpback whales reported to the Bureau of International Whaling Statistics as having been taken from the group IV and V populations since 1949.

At Australian whaling stations further material and data were collected from humpback whales by the author, other members of CSIRO, and the whaling inspectors. The most important of these items were the gonads and ear plugs required for studies of reproduction and age determination. The numbers of these collected in each year, and the percentage of the catch sampled for these organs, are shown in Table 3. Efforts were made to avoid bias in the sampling of the catches. During the earlier years most of the collections were made by a few research staff, seldom more than one member at a particular whaling station, so that it was not possible to examine all whales. Generally, whales processed during daylight and early evening were examined, without any preference being given to any particular category of whale. In recent years, the close cooperation of whaling inspectors has made it possible to examine the majority of the whales caught.

TABLE 1

HUMPBACK WHALES OF THE GROUP IV (70°E.–130°E.) POPULATION

Catches reported from 1949 to 1962

Year	Australian Shore Stations (quotas in parentheses)						Antarctic (pelagic)	Total Recorded Catch
	Point Cloates (22° 35′S., 113° 40′E.)		Carnarvon (24° 53′S., 113° 38′E.)		Albany (35° 05′S., 117° 56′E.)			
1949	(600)	190					0	190
1950	(600)	348	(600)	40			779	1167
1951	(600)	574	(650)	650			1112	2336
1952	(600)	536	(600)	600	(50)	51	1127	2314
1953	(603)	603	(600)	600	(100)	100	193	1496
1954	(600)	600	(600)	600	(120)	120	258	1578
1955	(500)	500	(500)	500	(126)	126	28*	1154
1956	Transferred to Carnarvon		(1000)	1000	(120)	119	832	1951
1957			(1000)	1018	(120)	102	0	1120
1958			(1000)	885	(120)	82	0	967
1959			(1000)	541	(175)	159	1413†	2113
1960			(750)	440	(120)	105	66	611
1961			(475)	475	(105)	105	4	584
1962			(540)	503	(100)	40	56	599
Total	West coast of Australia, 12,312						5868	18,180

* Reported as being killed illegally by F. F. *Olympic Challenger*.

† Redistributed after considering intermingling of populations IV and V (Chittleborough 1959).

The length frequency distribution of the whales examined generally did not differ significantly from the length frequency distribution of the catch from which the sample was taken, indicating that a representative sample of the catch had been taken. The ear plugs of the small whales were often soft and more difficult to remove intact than those of large whales. Consequently, the samples of ear plugs were less representative of the small whales (those less than 39 ft in length) as shown in Figure 5. This bias did not reach significant levels, except for the male ear plugs sampled on the east coast of Australia during 1961 (Fig. 5). In this case the length frequency distribution of the sample aged from ear plugs differed at the 1% level from that of the total catch of males.

Because of the difficulty of collecting ear plugs from the small (young) whales, the distribution of ages in the sample should not be stepped up by a constant ratio (total catch : number in sample) in order to obtain the distribution of ages in the whole catch. The best estimate of age distribution of the whole catch is obtained by applying the age to length key, derived from the sample, to the length frequency distribution of the whole catch. This technique has been applied in the estimation of age distribution of all catches from these populations (see Section V (*c*)).

TABLE 2

HUMPBACK WHALES OF THE GROUP V (130°E.–170°W.) POPULATION

Catches reported from 1949 to 1962

Year	Australian Stations (quotas in parentheses)						New Zealand	Antarctic (pelagic)	Total Recorded Catch
	Tangalooma (27° 11′S., 153° 23′E.)		Byron Bay (28° 37′S., 153° 38′E.)		Norfolk I. (29° 01′S., 167° 58′E.)				
1949							141	0	141
1950							79	903	982
1951							111	162	273
1952	(600)	600					122	146	868
1953	(700)	700					109	504	1313
1954	(600)	598	(120)	120			180	0	898
1955	(600)	600	(120)	120			112	1097*	1929
1956	(600)	600	(120)	120	(150)	150	143	194	1207
1957	(600)	600	(121)	121	(120)	120	184	0	1025
1958	(600)	600	(120)	120	(120)	120	183	0	1023
1959	(660)	660	(150)	150	(150)	150	318	885†	2163
1960	(660)	660	(150)	150	(170)	170	361	931	2272
1961	(660)	591	(150)	140	(170)	170	80	293	1274
1962	(600)	68	(150)	105	(170)	4	32	0	209
Total	Australia, 8307						2155	5115	15,577

* Reported as being killed illegally by F. F. *Olympic Challenger*.

† Redistributed after considering intermingling of populations IV and V (Chittleborough 1959).

(iii) *Treatment of Material*

Accounts have already been given of the methods used for the examination and interpretation of ovaries (Chittleborough 1954), testes, vertebral epiphyses (Chittleborough 1955), ear plugs, and baleen (Chittleborough 1959*c*).

In the description of ovarian changes, Chittleborough (1954) stated, with little supporting evidence, that Graafian follicles exceeding 30 mm in diameter were approaching ovulation. As this is an important criterion in distinguishing phases within the reproductive cycle, further corroboration is given in Figure 6 which shows the diameter of the largest follicle in 938 female humpback whales taken off the west coast of Australia from June to October. The modal diameter of 20 mm, characteristic of immature females, as well as of those in anoestrus and

TABLE 3

SAMPLES OF GONADS AND EAR PLUGS COLLECTED FROM AUSTRALIAN HUMPBACK WHALE CATCHES

West coast of Australia (group IV population)

Year	Males					Females				
	Total Catch	Testis Weight		Ear Plugs		Total Catch	Ovaries		Ear Plugs	
		Number	Percentage of Catch	Number	Percentage of Catch		Number	Percentage of Catch	Number	Percentage of Catch
1949	135	0	—	0	—	55	27	49·1	0	—
1950	250	0	—	0	—	137	32	23·4	0	—
1951	907	395	43·6	0	—	310	92	29·7	0	—
1952	666	161	24·2	0	—	516	278	53·9	0	—
1953	726	111	15·3	0	—	572	246	43·0	0	—
1954	692	7	1·0	0	—	617	150	24·3	0	—
1955	581	0	—	0	—	543	8	1·5	0	—
1956	676	110	16·3	32	4·7	443	279	63·0	12	2·7
1957	583	488	83·7	182	31·2	536	521	97·2	187	34·9
1958	509	439	86·2	233	45·8	458	438	95·6	219	47·8
1959	331	254	76·7	179	54·1	369	353	95·7	221	59·9
1960	271	208	76·8	139	51·3	274	263	96·0	155	56·6
1961	306	291	95·1	217	70·9	272	263	96·7	195	71·7
1962	304	280	92·1	186	61·2	239	230	96·2	134	56·1
Total	6937	2744		1168		5341	3180		1123	
East coast of Australia and Norfolk I. (group V population)										
1952	449	233	51·9	—	—	150	104	69·3	—	—
1953	509	200	39·3	—	—	191	121	63·4	—	—
1954	511	298	58·3	—	—	207	148	71·5	—	—
1955	494	37	7·5	—	—	226	118	52·2	—	—
1956	577	190	18·0	—	—	293	195	66·6	—	—
1957	585	267	45·6	204	34·9	256	198	77·3	94	36·7
1958	574	205	35·7	93	16·2	266	121	45·5	57	21·4
1959	633	273	43·1	236	37·3	327	252	77·1	125	38·2
1960	592	319	53·9	276	46·6	388	282	72·7	198	51·0
1961	572	569	99·5	379	66·3	329	304	92·4	197	59·9
1962	103	103	100·0	79	76·7	74	73	98·6	53	71·6
Total	5599	2698		1267		2707	1916		724	

metoestrus is clearly illustrated. A second peak at a follicle diameter of 42–45 mm which is shown in the results from mature (non-pregnant) females which did not carry a newly ruptured follicle nor a recently formed corpus luetum, was not present in the histogram for females which had recently ovulated. Maturation of a follicle from the resting (anoestrous) phase is apparently a rapid process, as there are few follicles from 27 to 36 mm in diameter (Fig. 6*b*). Females carrying a follicle exceeding 30 mm in diameter are approaching ovulation. On this basis, some of those females included in Figure 6*a* as immature, were in fact diagnosed as pubertal females killed during their first pro-oestrus.

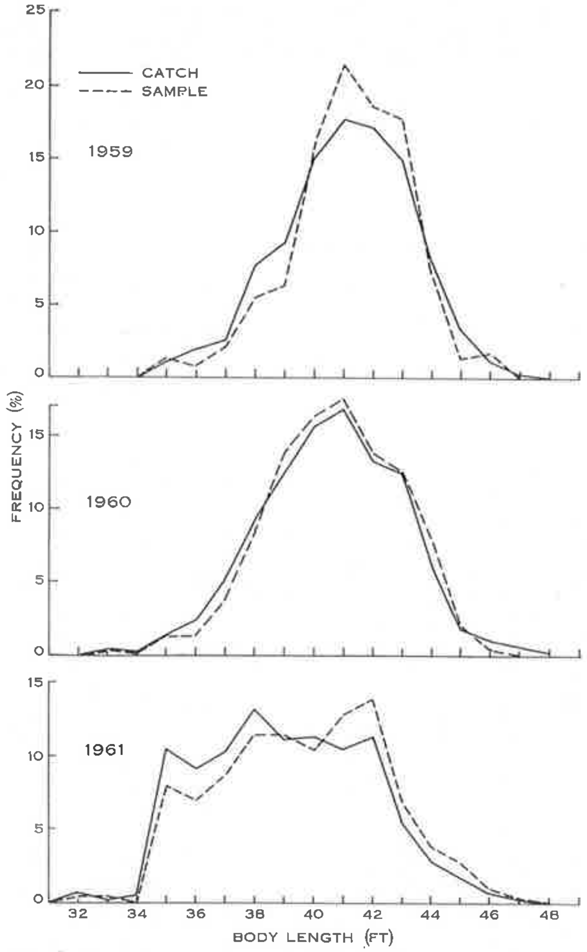

Fig. 5.—Male humpback whales from the east coast of Australia, 1959–61. Length frequency distribution of catch and of sample aged from ear plugs.

II. Identity of Populations

(*a*) *Geographic Limits, Ranges, and Migrations*

As reviewed by Mackintosh (1942), five more or less self-contained populations of humpback whales have been recognized in the southern hemisphere. Two of these are accessible to Australian shore-based whaling stations.

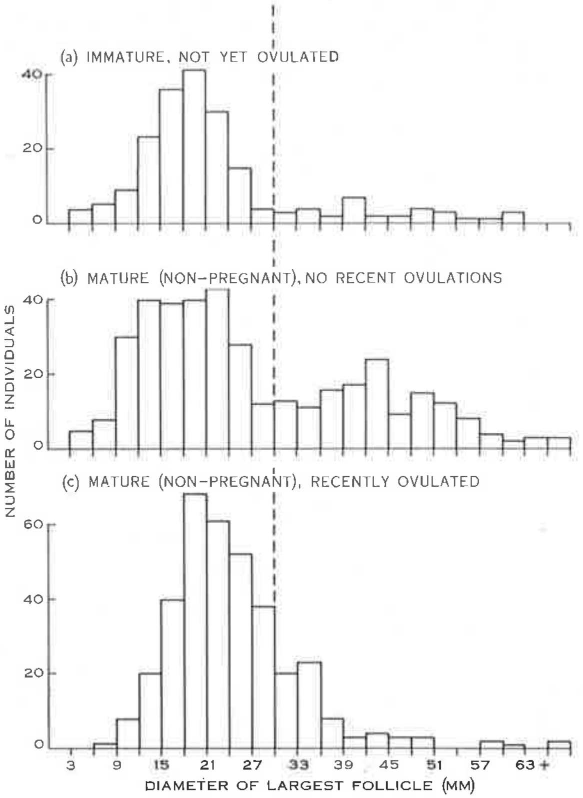

Fig. 6.—Diameter of largest Graafian follicle in each of 938 female humpback whales taken on the west coast of Australia between June and October.

Humpback whales which spend the winter months off the west coast of Australia, and the summer months concentrated in Antarctic waters in the vicinity of 80°E.–110°E. are known as the group IV population. The migration of these whales between the summer feeding grounds and the winter breeding grounds has been amply demonstrated by recapture of marked whales (Rayner 1940; Chittleborough 1959*a*). The meridional limits of this population are given as 70°E. and 130°E., but these cannot be regarded as rigid boundaries.

Humpback whales which in the summer months are concentrated in the Antarctic in the vicinity of 150°E.–180°E., and which migrate in the autumn to the east coast of Australia (Chittleborough 1959*a*) and the islands in the south-west

Pacific Ocean (Dawbin 1959), comprise the group V population. The meridional limits of this population are given as 130°E and 170°W., but there is some doubt as to the eastern limit of this range.

During the winter (breeding) season the majority of these humpback whales reach 20°S. latitude; Dawbin (1956) considers that most of the group V population reach 15°S. However, there is no particular latitude along the west and east coasts of Australia where migration ceases and breeding commences. Some individuals may migrate north of 10°S., while a few (late in their northward migration) may not reach 30°S. Parturition has been recorded as far south as Albany (35°S.); such females continue to move northwards during the first few weeks of lactation.

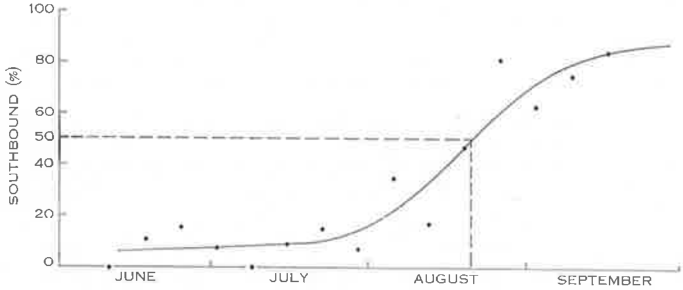

Fig. 7.—Proportions of southbound humpback whales in weekly sightings from the spotting aircraft operating from Point Cloates in 1953.

A few of those in the extreme vanguard of the northward migration may reach the Australian coast in April but the main part of the north-bound stream arrives in June. Figure 3 shows that on the east coast of Australia (in 1961) most of the northbound humpback whales passed 28°S. latitude during June and July, while a few stragglers were still making their way northwards as late as October. The southward migration took place mainly from the latter part of August until mid-October. The mid-point (in time) between the northward and southward migration (in that year) was close to August 15.

The group IV population migrates along the west coast of Australia at times similar to those at which migration occurs on the east coast. The northward migration past Albany (35°S.) is shown in Figure 4 (humpback whales do not pass Albany on their southward migration). At Point Cloates (22½°S.), the point in time mid-way between the northward and southward migration was close to August 24 in 1952 (Chittleborough 1953), and August 20 in 1953, as shown in Figure 7.

The time at which the migrating stream of humpback whales passes a particular locality varies slightly from year to year, as shown by Dawbin (1956) who compared the times at which the peak of the northward migration passed through Cook Strait, N.Z., in each of 35 years. The difference between the earliest of these (June 21 in 1947 and 1950) and the latest (July 29 in 1933) was 38 days. In the northward migration of group IV humpback whales past Albany (Fig. 4), the peak density was approximately 3 weeks earlier in 1959 than in 1956. Annual variation in the availability of food in the Antarctic (either by behaviour of the *Euphausia* themselves, or by climatic changes such as the formation of sea ice making the *Euphausia* inaccessible) might be responsible for these annual variations in the time of the northward migration, but there are no precise data concerning these conditions in the Antarctic.

The speeds at which individual humpback whales travel during undisturbed migration have been measured by direct (aerial) observations over periods of a few hours, giving speeds from 2·6 to 7·7 knots (Chittleborough 1953), the mean of the values being 4·3 knots. Similar speeds have been maintained for longer periods by humpback whales marked during their migration along the Australian coast; one travelled a minimum of 520 nautical miles during 6 days subsequent to marking (average speed 3·6 knots), while another travelled at least 430 nautical miles in 7 days (average speed 2·5 knots). That these speeds can be maintained over very considerable distances was demonstrated by a humpback whale marked when passing through Cook Strait, N.Z., on June 15, 1960, and shot 20 days later off Moreton I., on the east coast of Australia. The shortest distance between these points is 1350 nautical miles, so that this whale must have averaged at least 2·8 knots.

In contrast to these relatively rapid movements by individual whales are those of whales seen idling or playing with little active migration. Some whales may spend several days in one locality before continuing their migration. For example, a humpback whale marked on July 30, 1960, close to Norfolk I., was killed 10 days later in the same locality.

Dawbin (1956) calculated the average rate of progression of the whole population during migration from the times at which the maximum density of the northbound whales passed widely separated observation points. His figure of 1·3 knots is the rate of progression of the whole population in the course of its northward migration. Individuals may vary their speed from time to time, and sometimes change their direction temporarily. Some of the individuals shown in Figure 3 as migrating northwards during September and October may actually have been southbound whales which were milling around at the time observed.

Although most humpback whales have left the Australian coast by the end of October, some have been sighted in these waters in November and December. Three separate females seen migrating southwards along the west coast during December had probably been late in making the northward migration, each being accompanied by a calf (see Section II (*d*)). The appearance of such whales, late in making their way south, and of others exceptionally early in migrating from the southern feeding grounds, might have been what led Mackintosh to suggest (Mackintosh 1942, p. 238) that a few humpback whales remain in subtropical waters throughout the summer.

During the summer the group IV population feeds in the Antarctic between 56°S. and 66°S. latitude, and the group V population from 59°S. to 68°S. (Omura 1953).

(*b*) *Discreteness of Populations*

Very few humpback whales winter off the south coast of Australia. Occasionally an individual may terminate its northward migration at the head of the Great Australian Bight. Calaby (personal communication) sighted a humpback whale there (at 130° 30′E.) on August 3, 1952. A female humpback whale and its newborn calf were reported in St. Vincent Gulf, South Australia (138½°E.) during the winter of 1961. On the western side of Australia some humpback whales meet the south coast during their northward migration, but they then follow the coastline to the west and south-west (passing the whaling station at Albany) until they can continue their northward migration up the west coast. Humpback whales do not pass the station at Albany at the time of the southward migration.

Since almost all members of these populations are distributed along the coastlines to the north of 30°S. during the winter (breeding) season, there is complete reproductive isolation, as the two populations are separated at that time by the Australian continent.

The geographic distribution of catches from these populations during the summer (feeding) season (Omura 1953, fig. 9; Chittleborough 1959*b*, Table 3) would indicate that there is generally little exchange of individuals between these populations in Antarctic waters. Humpback whales are seldom captured in the region from 120°E. to 140°E. A reservation which must be made here is that in recent years the period of open season for humpback whales in the Antarctic has been so brief (4 days) that the location of catches reflects the positions of factory ships at that time. Whaling masters endeavour to place their vessels in regions of greatest density of whales, and if already operating successfully on fin whales, they would not move the fleet for the short season on humpback whales.

The composition of the catches taken from the group IV and V populations from 1949 to 1954 affords evidence that there was little interchange between these populations. During this period the lengths of males and females taken each year decreased both in the catches from the northern (west coast of Australia) and southern (Antarctic area IV) ranges of the group IV population (Chittleborough 1958*a*). On the other hand, the sizes of whales taken from both the east coast of Australia and from Antarctic area V remained at similar high levels during those years.

The migrations by individuals from these populations are demonstrated from the subsequent recapture of humpback whales marked off the Australian coast (Table 4, and also Chittleborough 1959*a*), near islands in the south-west Pacific Ocean (Dawbin 1959), and in Antarctic waters (Rayner 1940). The intervals between marking and recapture of these whales ranged from a few days up to 17½ years. Only those killed 6 months or more after marking can be considered to have had an opportunity to move from one population to another.

Of the humpback whales marked when within the territory of the group IV population (70°E.–130°E.), 56 have been recaptured after 6 months or more. Of these, 54 (96·4%) had remained in the group IV population, while the remaining two had entered the confines of the group V population.

Of the humpback whales marked when within the territory of the group V population (130° E.–170° W.), 84 have been recaptured after 6 months or more. Of these, 73 (86·9%) had remained in the group V population, 10 (11·9%) had moved into the area of the group IV population, while one had joined the group I population (120 °W.–60 °W.).

TABLE 4

HUMPBACK WHALES MARKED OFF AUSTRALIA AND ALL KNOWN RECAPTURES FROM THESE UP TO 1962

Marked Whales		Recaptured Whales (number of years after marking)																
Year	Number Marked	Locality	0	½	1	1½	2	2½	3	3½	4	4½	5	5½	6	6½	7	9
(A) Humpback whales marked off east coast of Australia (group V population)																		
1950	4	—																
1952	4	—																
1953	14	Eastern Australia	1						1									
1954	66	Eastern Australia	1		1		2											
		Antarctic Area V										1				1		
		Western Australia											1					
1955	180	Eastern Australia	3		3		1		9		3							
		New Zealand											1					
		Antarctic Area V												1				
		Antarctic Area IV								2								
		Western Australia									1							
1956	376	Eastern Australia					2		3		3		2					
		New Zealand			1													
		Antarctic Area V						2				1						
		Antarctic Area IV						3										
1957	63	Eastern Australia	1															
		New Zealand					1											
1958	123	Eastern Australia	1		2		1		1									
		Antarctic Area IV		1														
1959	57	Eastern Australia			1		1											
		Antarctic Area V				1												
1960	116	Eastern Australia					1											
		Antarctic Area V		1														
1961	34	Eastern Australia	1															
1962	4	Eastern Australia	1															
(B) Humpback whales marked off west coast of Australia (group IV population)																		
1949	16	Western Australia					1											1
1954	21	Western Australia					1											
1955	69	Western Australia	1				1		1						1			
		Antarctic Area IV		1														
1956	6	Western Australia							1									
1957	80	Western Australia			1						1							
		Antarctic Area IV				2												
1958	46	Western Australia									1							
1960	12	—																
1961	20	—																
1962	17	—																

During the period of study the exchange between the group IV and group V population took place mainly in the summer feeding season of 1958–59. Chittleborough (1959*b*) has shown that catches of humpback whales taken during February 1959 from the eastern portion of the Antarctic feeding grounds of the group IV population (i.e. from 110°E. to 130°E.), comprised approximately equal numbers of individuals from the group IV and group V populations. That there had been an expansion of the feeding area of the group V population in that summer was confirmed by the capture in the eastern part of the group IV sector, of eight humpback whales marked when in the normal range of the group V population.

The movement between these two populations during the summer of 1958–59 has been further clarified by the results from the recoveries of marks fired during that summer. Figure 1 illustrates the movements of marked whales which were either marked or killed in the summer of 1958–59 or the following winter. During the summer of 1958–59 the group V population extended its feeding range to overlap the feeding area of the group IV population (which apparently had not been dispersed any more widely than usual). During the autumn, the majority of the members of the group V population which had penetrated the eastern part of the feeding grounds of the group IV population, returned to the normal range of the group V population, migrating to the east coast of Australia. However, some (at least two) of the group V population remained with the group IV population and migrated to the west coast of Australia (Fig. 1). The differences in abundance of whales, and in the composition of catches on the west and east coasts of Australia during the winter of 1959 (Chittleborough 1960), suggest that very few individuals from the group V population had remained with the group IV population during the autumn northward migration.

The evidence of humpback whale sightings, catches, catch composition, and of movements of marked whales, indicates that these populations remain separate in most years. Intermingling occurs occasionally in the southern feeding grounds, but this does not lead to much permanent exchange between the populations (perhaps because of some inherent instinct of individuals to return to the locality where they were born).

Little is known of the factors responsible for maintaining the discreteness of southern humpback whale population in Antarctic waters during the summer feeding season. Beklemishev (1960, 1961) has postulated that humpback whales gather to feed on concentrations of *Euphausia superba* brought to the surface in centres of upwelling induced in the Antarctic Divergence by atmospheric cyclones. These cyclones are reputed to be quasi-stationary and to re-form in the same localities, concentrations of krill being brought to the surface in the centres of upwelling so produced. If this is the mechanism by which populations of humpback whales remain separated during the feeding season, we might interpret the wider dispersion of the group V population during the summer of 1958–59 as having been caused by poor development of the system of quasi-stationary cyclones in the vicinity of the Balleny Is. (160°E.) at that time.

(*c*) *Morphological Differences*

Lillie (1915) distinguished seven colour patterns (four main and three intermediate groups) in humpback whales, these patterns ranging from completely black bodies (given as group 4) to individuals having white skin on the abdomen and sides (group 1). By comparing the frequency of occurrence of the various colour patterns, Matthews (1938) showed that humpback whales from South Georgia and South Africa (populations II and III) were predominantly of the darker patterns, while those from new Zealand (population V) were generally less pigmented. Using these seven colour patterns, Omura (1953) produced further evidence of a progressive decrease in pigmentation amongst Antarctic humpback whales from the South Atlantic eastwards towards the Ross Sea.

TABLE 5

FREQUENCY OF OCCURRENCE OF FOUR COLOUR PATTERNS IN HUMPBACK WHALES SAMPLED FROM VARIOUS LOCALITIES

Locality	Sample		Frequency of Colour Pattern (%)			
	Sex	Number	1	2	3	4
S. Georgia and S. Africa (Matthews 1938)	Male	25	4·0	12·0	16·0	68·0
	Female	28	0·0	3·6	17·9	78·6
West coast of Australia	Male	599	16·2	34·1	32·9	16·9
	Female	428	13·8	36·2	32·0	18·0
East coast of Australia	Male	619	29·4	36·9	19·9	13·7
	Female	281	30·5	39·9	15·1	14·4

Because observers differed in their interpretation of the ill-defined intermediate patterns, only the four main colour patterns figured by Lillie and Matthews are used in comparison of Australian samples (Table 5). Figure 8 shows that although the complete range of colour patterns is found in each population, the less pigmented individuals are more plentiful in the group V population (east coast of Australia) than in the group IV population (west coast of Australia), while in the South Atlantic Ocean (group II and III populations) most individuals are heavily pigmented ventrally as well as dorsally.

Measurements were made of various parts of the bodies of humpback whales killed on the west and east coast of Australia, in order to determine whether members of these two populations differed significantly in body form. Statistical analysis of these measurements showed greater differences between the measurements taken by two observers measuring whales from the same population than between measurements from whales of the two populations.

Although these two populations of humpback whales are separate entities, there is apparently sufficient interchange between them to prevent genetic differences from reaching significant levels. Thus there is little justification for the separation of races or subspecies of humpback whales within the southern hemisphere, as has been done by Ivashin (1958).

(*d*) *Segregation within Populations*

(i) *Sub-division of Breeding Grounds*

While the group IV population has only one breeding area (along the west coast of Australia), the group V population is widely dispersed during the breeding season. A large portion of the group V population breeds along the east coast of Australia, but other members gather around island groups of the south-west Pacific Ocean. Dawbin (1959) postulated from the movements of marked

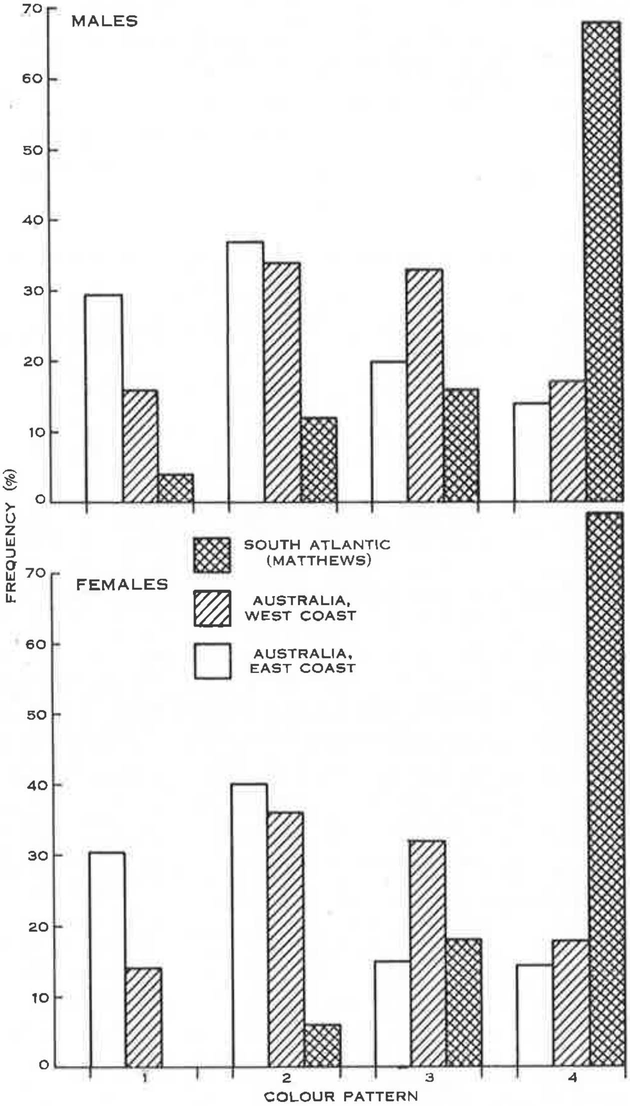

Fig. 8.—Frequency distribution of four colour patterns amongst humpback whales sampled from populations II–III (South Atlantic), IV (west coast of Australia), and V (east coast of Australia).

whales recaptured up to 1958, that this population of humpback whales did not disperse at random across the width of the tropical breeding zone, but that individuals generally returned to the same coastline or island group year after year. From these results, Dawbin suggested that the population was segregated to some extent into a number of breeding units and that the individuals usually returned to breed in the locality where they had been born and weaned.

The total numbers of humpback whales marked (up to 1960) in the northern area of distribution of this population were 946 on the east coast of Australia and 875 off the south-west Pacific islands. If these whales returned to the locality of marking (after mingling freely in the Antarctic feeding area), then whaling on the east coast of Australia should recover only marks implanted off that coast. However, if the whales remained randomly dispersed in their northward migration, whaling on the east coast of Australia should yield marks from both the east coast of Australia and the south-west Pacific islands, in the proportion 946 : 875. Table 6 shows the recoveries of marks on the east coast of Australia in recent years and compares their origins, as observed, with what would be expected by the hypothesis that the marks from the two regions would be randomly distributed. Recoveries on the east coast of Australia during 1959 would support the theory of segregation of breeding grounds within this population, whereas the recoveries on this coast in 1960 and 1961 support the hypothesis of random distribution during the breeding season.

From the recoveries of marks up to 1959 there may have been partial segregation of breeding grounds within the group V population, but this appears to have broken down in 1960 and 1961.

(ii) *Segregation during Migration*

Chittleborough (1958*b*) and Dawbin (1960) showed that during the northward migration the whales of certain categories within the population travel ahead of others. These authors were not able to measure the abundance of one category relative to another throughout the migration past the particular points. This is now shown in Figure 2 for the population passing Albany (35°05′S.) on the south-west coast of Australia during the combined northbound migrations from 1952 to 1961. As set out in Table 7, the mean catch per 10 steaming hours within 7-day periods is used as an index of the abundance of each category. Because of the minimum legal length (35 ft), the immature groups are not fully vulnerable, so that the values shown in Figure 2 and Table 7 for immature groups are instead the abundance of those exceeding 35 ft.

Figure 2 shows that sexually immature individuals and mature females terminating lactation are in the vanguard of the northward migration. Non-pregnant mature females (those which had been in non-lactation anoestrus, and others which had completed lactation) continue to pass throughout the period of the northward migration, while pregnant females (carrying near-term foetuses) are in the rear of the northward migration. Adult males are most abundant in the centre of the migration, and continue to be relatively plentiful in the latter portion of the migrating stream.

Segregation of the various categories during the northward migration may be the result of each leaving the Antarctic feeding grounds at a different time. There is no indication that individuals within a particular category travel at a higher average speed than those in any other.

Partial segregation of the various categories of humpback whales is apparently continued during the southward migration, those which were first to arrive in temperate and tropical waters being the first to depart on the southward migration. The pregnant females, which were amongst the last to migrate northwards (Fig. 2), gave birth on reaching warmer waters (Chittleborough 1958*c*), and were then amongst the last to migrate southwards (Chittleborough 1953, and also Fig. 3 above).

TABLE 6

RECENT RECOVERIES ON THE EAST COAST OF AUSTRALIA OF MARKS FIRED ON OR NEAR THE BREEDING GROUNDS OF THIS POPULATION

Year of Capture	Total Marks Recovered	Origin of Marks			
		East Coast of Australia		S.W. Pacific Is.	
		Observed	Expected*	Observed	Expected*
1959	8	8	4·16	0	3·84
1960	9	5	4·68	4	4·32
1961	7	4	3·64	3	3·36

* On the hypothesis of random distribution.

The main stream of humpback whales migrating past Australian shore stations passes within 10 miles of the coast; few humpback whales are seen or captured more than 20 miles from land in the vicinity of these stations, in spite of much wider ranging of searching aircraft and vessels operating from these stations in recent years. The various categories of humpback whales listed in Table 7 are dispersed across the width of the migrating stream, no group being confined either inshore or staying further offshore than any other group.

III. LIFE HISTORY

(*a*) *Reproduction*

(i) *Puberty*

From the histological examination of testes, Chittleborough (1955*a*) showed that the length of the males at puberty ranged from 33·3 to 40·8 ft with a mean of 36·75 ft. The average weight of the paired testes at this stage was 4·0 kg.

From the ages determined from baleen traces of 238 male humpback whales, Chittleborough (1959*c*) showed that the mean age of males at puberty was between 4 and 5 years, more males reaching puberty at 5 than at 4 years of age. Further evidence upon the ages of males at puberty is given in Figure 9 which shows the growth of testes (by weight), based on the data from 1067 males. Using the testes weight

TABLE 7

RELATIVE ABUNDANCE, AS INDICATED BY CATCH PER UNIT EFFORT, OF VARIOUS CATEGORIES OF HUMPBACK WHALES THROUGHOUT THE NORTHWARD MIGRATION PAST ALBANY (35°05′S.)

Combined data from 1064 humpback whales taken from 1952 to 1961

Week Ending:	Total Effort (steaming hours)	Total Catch (humpback whales)	Catch per 10 Steaming Hours	Catch Cagetory											
				Mature Females						Immature Females		Immature Males		Mature Males	
				Non-pregnant				Pregnant (near-term)							
				Terminating Lactation		Post-lactation									
				Number Killed	Catch per 10 Steaming Hours	Number Killed	Catch per 10 Steaming Hours	Number Killed	Catch per 10 Steaming Hours	Number Killed	Catch per 10 Steaming Hours	Number Killed	Catch per 10 Steaming Hours	Number Killed	Catch per 10 Steaming Hours
May 28	87·5	1	0·11	1	0·11	0	0	0	0	0	0	0	0	0	0
June 4	204·2	5	0·24	1	0·05	0	0	0	0	1	0·05	2	0·10	1	0·05
11	584·8	30	0·51	11	0·19	2	0·03	0	0	8	0·14	6	0·10	3	0·05
18	915·2	65	0·71	19	0·21	6	0·07	0	0	18	0·20	12	0·13	10	0·11
25	1038·2	113	1·09	24	0·23	7	0·07	0	0	30	0·29	18	0·17	34	0·33
July 2	962·8	115	1·19	14	0·15	4	0·04	2	0·02	20	0·21	24	0·25	51	0·53
9	1051·2	170	1·62	14	0·13	12	0·11	8	0·08	29	0·28	30	0·29	77	0·73
16	1090·2	174	1·60	11	0·10	32	0·29	6	0·06	24	0·22	29	0·27	72	0·66
23	883·2	120	1·36	1	0·01	25	0·28	15	0·17	13	0·15	15	0·17	51	0·58
30	946·2	109	1·15	0	0	21	0·22	18	0·19	17	0·18	6	0·06	47	0·50
Aug. 6	854·0	80	0·94	0	0	20	0·23	20	0·23	3	0·04	3	0·04	34	0·40
13	477·2	40	0·84	0	0	6	0·13	16	0·34	3	0·06	1	0·02	14	0·29
20	413·2	31	0·75	0	0	6	0·15	9	0·22	1	0·02	2	0·05	13	0·31
27	106·2	8	0·75	0	0	0	0	3	0·28	0	0	0	0	5	0·47
Sept. 3	62·5	3	0·48	0	0	1	0·16	1	0·16	0	0	0	0	1	0·16
Total		1064		96	1·18	142	1·78	98	1·75	167	1·84	148	1·65	413	5·17

of 4·0 kg as a criterion, puberty can be said to be reached at 3–6 years of age, 11·8% being mature at 3 years, 33·0% at 4 years, 85·4% at 5 years, and 95·0% at 6 years.

From an examination of females captured during their first oestrous cycle, Chittleborough (1955*b*) found that females at puberty ranged in size from 35·2 ft to 43·5 ft, with a mean length of 38·50 ft. Subsequently, Chittleborough (1960*b*) showed that the mean length of pubertal females taken in the catch varied with the degree of selection applied by gunners, and that after a period of intensive and selective killing, the capture of the slower growing individuals remaining in the population, resulted in an apparent decrease in the mean length at puberty.

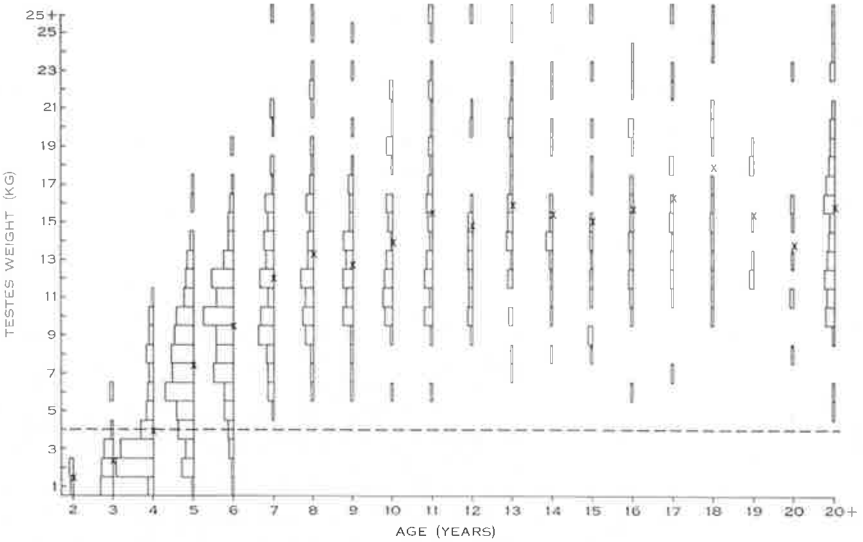

Fig. 9.—Distribution of testes weights and mean of each age group (×) in 1067 male humpback whales from Australia. Ages by ear plugs.

In New Zealand, under conditions of minimum selectivity, Dawbin (1960) estimated the average length at the attainment of sexual maturity to be 38 ft for males and 39·5 ft for females. These whales were killed early in the northward migration, so that pubertal whales were not available for study. Chittleborough (1955*b*, p. 318) showed that the mean length of females reaching sexual maturity (1 year after puberty), on the west coast of Australia, was 39·66 ft.

From the ages determined from the baleen traces of 391 female humpback whales, Chittleborough (1959*c*) showed that the majority of females reach puberty at 4 and 5 years of age. Further evidence upon the ages of females at puberty is given in Figure 10, which is based upon the data from 1603 females whose ovaries and ear plugs were examined at Australian stations. While the ages at puberty range from 2 years to a (doubtful) extreme of 12 years, the majority of individuals (70%) attain puberty at 4 and 5 years of age. No indication has been found of any significant variation in age at puberty from year to year or between the group IV and group V populations.

(ii) *Breeding Season*

Male humpback whales undergo a seasonal sexual cycle, as evidenced by changes in testes weight and spermatogenesis. Chittleborough (1955*a*), Symons and Weston (1958), and Nishiwaki (1959) have shown that testes weights are lower in males taken in polar waters during the summer (feeding season) than in those captured in temperate and subtropical waters during winter months (breeding season). Matthews (1938) and also Symons and Weston found very little testicular activity during summer months when the males were in Antarctic waters, while spermatozoa were plentiful both in testes tubules and in vasa deferentia of adult males taken off the Australian coast from June to October (Chittleborough 1955*a*).

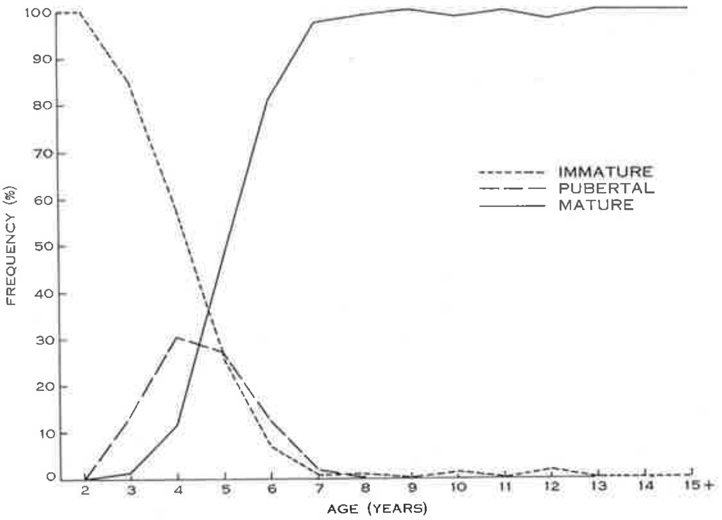

Fig. 10.—Percentages of sexually immature, pubertal, and mature females in each age group; data from 1603 female humpback whales from Australian stations.

Because of this seasonal activity of testes, the relationship between testes weight and age, shown in Figure 9, is valid only for the duration of the breeding season. The mean testes weight of 4·0 kg at puberty may not be applicable to males taken in polar waters, or even in New Zealand during the early part of the northward migration. This may account for the somewhat higher lengths of males at maturity estimated by Dawbin (1960) in New Zealand and by Omura (1953) in the Antarctic both of whom used the testes weight of 4 kg as the criterion of maturity.

Contrary to Harvey's (1963) interpretation of the evidence given by Chittleborough (1954), female humpback whales are seasonally polyoestrus. Most oestrous cycles occur during the winter and early spring (June–October in the southern hemisphere) when the whales are in temperate and subtropical waters. There may be one or several successive cycles, terminated when conception succeeds or when the female migrates to the polar feeding grounds. In each oestrous cycle there is generally a single ovulation but multiple ovulations (seldom involving more than two follicles) occur occasionally.

The average rate of ovulation is 1·1 ovulations per year (Chittleborough 1959*c*), but the distribution (in time) of ovulations during the 2-year breeding cycle has not been fully elucidated. Chittleborough (1959*c*, Table 5) estimated that during the first ovulatory season of the 2-year breeding cycle, there was an average of 1·2 ovulations per mature female. If this were so, a very high percentage of females should have a post-partum ovulation in order to achieve an average annual rate of 1·1 ovulations per year. However, Dawbin (personal communication) who has examined the ovaries of female humpback whales killed (by Tongan natives) soon after parturition, found no evidence that post-partum ovulation is of frequent occurrence in this species. Because of this, the actual rate of ovulation at the commencement of a 2-year breeding cycle may be higher than 1·2 ovulations per female.

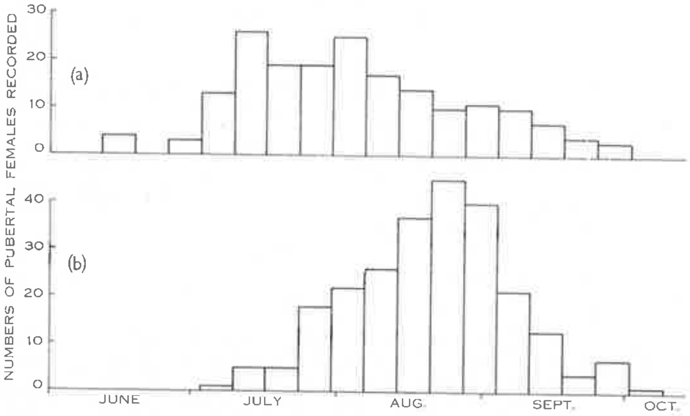

Fig. 11.—Distribution in time of 432 pubertal females killed (*a*) shortly before, (*b*) soon after the first ovulation, during operations throughout the Australian season.

Re-examination of ovarian material collected during the ovulatory period has led to the conclusion that in the ovaries of a female killed during the second or third successive oestrous cycle of a season, involution of the first corpus luteum had in many cases proceeded to the extent that it was classed as a corpus albicans (of an ovulation in a previous season). Robins (1960) presented evidence that an average of 1·48 ovulations occurred in females during the breeding season at the commencements of the 2-year breeding cycle, but he then regarded this as the average annual rate of ovulation.

Laws (1961) suggested (from indirect evidence) that oestrus and pairing in the fin whale took place later in the season for primiparous females than for multiparous females. This can be checked by direct observation in the case of humpback whales taken at Australian shore stations. Although immature females (of all sizes) are present in Australian catches during June (Fig. 2), very few have the maturing follicle which would indicate prooestrus of the first oestrous cycle. Females in this condition (approaching their first ovulation) are taken more frequently during July and in early August (Fig. 11). Most of the pubertal females had ovulated by mid-August, although a few did not ovulate until October. From this evidence, obtained from 432 pubertal females, the first ovulation can occur between June and October, but most ovulate early in August. This is almost the same result as that obtained by Chittleborough (1956) for multiparous female humpback whales.

The timing of the first ovulation did not vary from year to year, nor did it differ in the two breeding regions under study (west and east coasts of Australia).

(iii) *Pregnancy and Lactation*

The gestation period is of approximately 11½ months, conception generally occurring early in August, and parturition at the end of the following July or the beginning of August (Chittleborough 1958*c*), both conception and parturition taking place along the coasts of Australia. Embryonic and early foetal stages have been described by Stump, Robins, and Garde (1960). A foetal growth curve for this species is given by Laws (1959). Generally a single foetus is carried; Chittleborough (1958*c*) recorded twins in 0·28% of pregnancies. The modal length at birth is 14 ft (4·3 m) (Chittleborough 1958*c*). Caudal presentation at birth has been described by Dunstan (1957).

Lactation extends over 10½–11 months (Chittleborough 1958*c*), weaning taking place during June and early July as the whales reach temperate latitudes (Fig. 2 of this paper). During their first Antarctic summer, calves from 6 to 9 months of age might supplement their milk diet with euphausiids, but there is no definite evidence of this.

Sharks and killer whales are probable causes of mortality among calves (Chittleborough 1953). If the calf is lost at or close to the time of parturition, oestrous cycles recommence (Chittleborough 1958*c*). Oestrus can follow parturition while the female is suckling a calf but, as discussed in the previous section, post-partum ovulation is probably not of regular occurrence in this species.

(iv) *Rate of Reproduction*

The breeding cycle of the female humpback whale is basically a 2-year one (Chittleborough 1958*c*), variations of which can result in either one or two calves being born in that time. However, successive breeding cycles do not necessarily follow immediately one after another; a resting year (when a female is neither pregnant nor lactating) may intervene between two cycles.

The reproductive rate could be measured if the corpora albicantia derived from previous pregnancies could be distinguished from those of ovulations which did not lead to pregnancy. Various attempts have been made to separate corpora albicantia into these two categories. Robins (1954) suggested that corpora albicantia from an earlier pregnancy are characterized by a central cavity or capsule of connective tissue. However, Laws (1958) and Ivashin (1957) do not accept this theory. Ivashin claimed that the two types of corpora albicantia could be distinguished by size, density, texture, and content of connective tissue, but his descriptions are very similar to the "young" and "old" stages of corpora albicantia involution described by Laws. To date, there is no reliable method by which corpora albicantia can be separated into those derived from pregnancy and those from unsuccessful ovulations.

A direct measure of the birth rate is the percentage of mature females found to be pregnant among those killed just prior to the period when parturition occurs. The whaling station at Albany is suitably located for such observations, as the population passes shortly before parturition occurs. The fishing effort expended has fluctuated from week to week during a season, and also from one season to another, operations sometimes terminating before the pregnant females had passed. These difficulties were resolved by expressing the abundance of pregnant and non-pregnant mature females in weekly periods throughout the season, in terms of catch per unit of effort, as shown in Table 7. From these values, the total relative abundance of non-pregnant mature females was 2·96 units, and that of pregnant females was 1·75 units. Then, 1·75 : 4·71 or 37·2% of the mature females give birth each year, i.e. the average annual birth rate is 0·37 in this species.

(*b*) *Nutrition*

(i) *Food and Feeding*

The most important item in the diet of humpback whales is *Euphausia superba* which is taken in large quantities in Antarctic waters during summer and autumn (Matthews 1938; Mackintosh 1942; Mizue and Murata 1951; Nemoto 1959). Nemoto and Nasu (1958) found that *Thysanoessa macrura* was of some importance in the diet of humpback whales in Antarctic waters between 130°W. and 100°W.

According to Beklemishev (1960, 1961) humpback whales gather to feed upon late larval and adolescent *Euphausia superba* which are concentrated in regions of upwelling along the Antarctic Divergence. These centres of upwelling are considered to be produced by quasi-stationary cyclonic depressions which re-form in the same localities. Klumov (1961) estimated that humpback whales feeding in polar waters consume 1–1·5 tons of euphausiids per day. He postulated that dense concentrations (exceeding 2000 mg/m^3) of these organisms are actively sought by the whales using echolocation, vision, and touch.

Fish have been recorded occasionally in the stomachs of humpback whales (Matthews 1937; Nishiwaki 1959; Nemoto 1959) but in these instances the fish may have been swallowed accidentally by the whale while both fish and whale were feeding on the plankton.

In somewhat warmer waters, the pelagic *Grimothea* post-larvae of *Munida gregaria* are eaten while humpback whales are migrating along the coast of Patagonia (Matthews 1932) and New Zealand (Dawbin and Falla 1949; Dawbin 1956). Dawbin points out that off New Zealand the humpback whales could feed on *Grimothea* only during the southward migration of the whales, as shoaling of these post-larvae does not commence until late in the spring. During their northward migration past New Zealand, humpback whales occasionally take *Nyctiphanes australis*.

Humpback whales seldom find sufficiently dense swarms of plankton off the Australian coast to stimulate feeding. Dall and Dunstan (1957) recorded food present in only one of over 2000 humpback whales examined at Tangalooma. However, the stomachs of these whales were examined rather superficially; when only small amounts of foods are present, the remnants of this food may escape recognition unless the stomach contents are strained and the residues examined minutely. Close examination of the stomach contents from 197 humpback whales sampled at Carnarvon and Point Cloates (west coast of Australia) showed food remains in five of those taken off Point Cloates. In each of these whales the quantity of food ingested was small (probably less than 2 kg before decomposition began). Several species of food organisms were present in each case indicating that a small swarm of mixed plankton had been eaten. The most common species were *Euphausia hemigibba* and *Pseudeuphausia latifrons*. Other organisms noted were alima larvae of a stomatopod, probably *Gonodactylus* sp., megalopa larvae, a large caridean larva, and salps—*Ghalia democratica.*

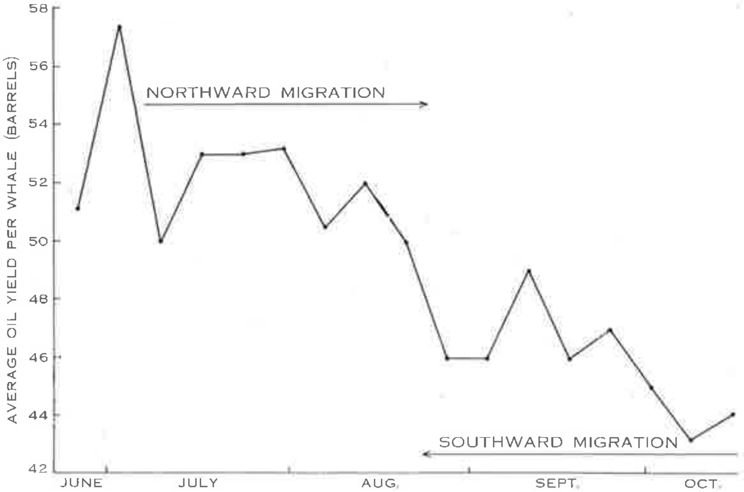

Fig. 12.—Average weekly oil yield per whale at Carnarvon in the 1958 season.

A female humpback whale taken off Albany in July, 1955, carried approximately 10 kg of *Euphasia spinifera* in very fresh condition.

The discovery of a large mass of semi-digested *Euphausia superba* in the stomach of a humpback whale at Tangalooma (27 °S.) in July, 1956 (Dall and Dunstan 1957), stimulated some debate (Jonsgård 1957; Marr 1957) as to whether the bathypelagic range of this Antarctic euphausiid should be extended, or whether the whale had carried this large sample 2400 miles from the Antarctic feeding grounds (the latter possibility appears to be the more favoured).

Humpback whales may occasionally ingest some plankton during their winter migration to temperate and subtropical waters but the total food intake is negligible for at least 4 months of each year. During this period the whales subsist on stored fat reserves, with the result that oil yields decline progressively at whaling stations in low latitudes, as demonstrated in Figure 12.

(ii) *Oil Yield*

The quantity of oil which can be extracted from each whale is influenced by the following factors:

(1) The efficiency of the factory. Factory efficiency varies not only from one shore station or factory ship to another but may also vary at a particular factory from one season to another, due to changes in equipment (e.g. depreciation on the one hand, or more skilful operation of the plant, or addition and replacement of machinery on the other).

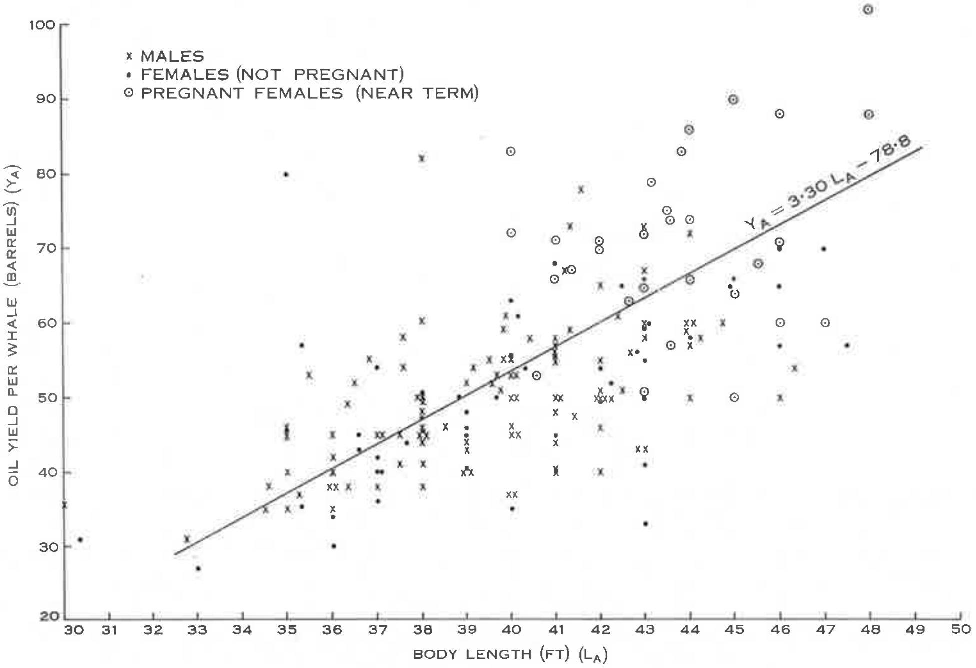

Fig. 13.—Oil yield and body length of individual humpback whales processed at Albany during 1953 and 1954.

(2) The size of the whale. Larger whales obviously carry more oil, as shown in Figure 13.

(3) Time and place of capture. The highest oil yields could be expected from whales killed when they have spent the summer feeding in the Antarctic, just before they depart on the northward migration. In temperate regions, whales are fatter as they pass a station on their northward migration, than when returning southwards at the end of a breeding season, as shown in Figure 12.

(4) Sex or phase of breeding cycle. Female humpback whales grow to larger size, and hence yield more oil, than males of similar ages. Mature females carrying near-term foetuses have been considered by whalers to yield more oil than other mature females.

(5) Availability of food. Humpback whales feeding in one area of the Antarctic may have access to more food (*Euphausia* more abundant, or less intraspecific or interspecific competition for food) than is the case in an adjacent population of humpback whales. Food supply may fluctuate from one year to another, so that whales from a particular population may be fatter in one season than in another.

The effects of these variables could only be measured if the oil yield had been recorded for each whale processed, together with details of the size, sex, breeding phase, date, and locality when killed. However, processing of whales at most factories has been rapid and continuous, so that the yield could not be measured for each whale.

TABLE 8

MEAN LENGTH AND AVERAGE OIL YIELD PER WHALE FROM ANNUAL CATCHES OF HUMPBACK WHALES AT VARIOUS WHALING STATIONS

Year	Point Cloates		Carnarvon		Albany		Tangalooma		Byron Bay		Norfolk I.		Cook Strait (N.Z.)
	Mean Length (ft)	Oil (barrels per whale)	Mean Length (ft)	Oil (barrels per whale)	Mean Length (ft)	Oil (barrels per whale)	Mean Length (ft)	Oil (barrels per whale)	Mean Length (ft)	Oil (barrels per whale)	Mean Length (ft)	Oil (barrels per whale)	Oil (barrels per whale)
1950	40·35	42·7	41·48	41·3	—	—	—	—	—	—	—	—	36·0
1951	40·27	43·2	40·31	47·8	—	—	—	—	—	—	—	—	40·4
1952	40·30	52·4	40·16	52·5	42·07	62·9	40·45	48·3	—	—	—	—	39·3
1953	39·91	50·7	39·59	50·6	39·86	51·9	40·36	51·4	—	—	—	—	41·8
1954	39·57	47·0	39·48	48·3	40·30	52·1	40·26	53·4	40·71	42·5	—	—	49·0
1955	40·35	49·8	41·32	50·6	40·20	47·6	40·70	54·5	42·10	57·2	—	—	44·8
1956	Closed		41·23	50·1	40·25	49·3	40·98	54·5	41·32	53·2	41·61	45·5	43·3
1957	—	—	40·77	50·6	39·56	49·4	40·89	57·5	39·91	42·1	41·52	55·1	46·5
1958	—	—	40·43	49·6	38·74	47·1	41·18	59·8	41·93	59·9	42·32	51·0	45·0
1959	—	—	38·76	45·1	39·63	49·8	41·17	59·1	42·44	58·1	41·34	52·0	50·3
1960	—	—	38·94	47·0	38·50	47·4	40·81	55·3	41·95	52·0	41·18	46·9	37·6
1961	—	—	37·54	45·8	37·94	48·0	38·76	42·8	40·68	49·1	41·01	44·4	47·8
1962	—	—	38·27	44·0	38·63	46·4	37·95	41·0	38·51	35·3	*	—	†

* Only four humpback whales taken.
† Data not available.

The station at Albany was unique in this regard. Having a small quota of humpback whales and very limited factory capacity (at least in the early years of operations), approximate quantities of oil extracted from individual whales were sometimes estimated at this station. Oil yield (Y_A) plotted against length of whale (L_A), as shown in Figure 13, gave the relation:

$$Y_A = 3{\cdot}30\ L_A - 78{\cdot}8.$$

For the reasons discussed above, this result is applicable only to humpback whales taken by that station (35°05′S.) during the northward migration of the group IV population in 1953 and 1954. Most of the pregnant females represented in Figure 13 would have given birth (and hence become protected by law) before migrating much further north. With those females no longer vulnerable, and assuming that there had been no other change in the catch or factory efficiency, the relation between oil yield and length would then have been:

$$Y_{\mathrm{A}} = 2{\cdot}85\ L_{\mathrm{A}} - 60{\cdot}5.$$

At other whaling stations, oil yields from individual whales could not be determined. From the total oil produced each season, the mean production per whale could be estimated (Table 8). At most stations the average oil production per whale was less in the first season of operation than in the second, and thereafter varied with the mean length of the catch. Other factors, such as length of catching period, sex ratio, breeding season, fluctuations in food supply, etc., appear to have been of less importance, but the degree of influence of these factors could not be measured.

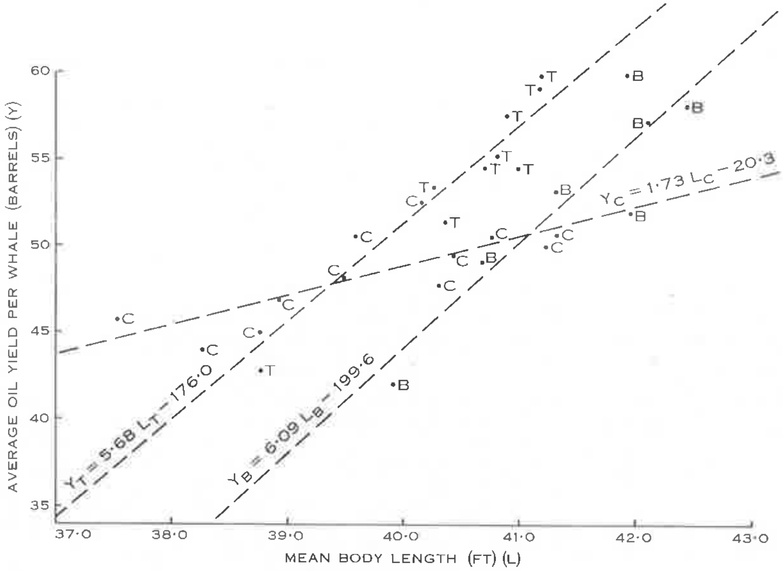

Fig. 14.—Regression of oil yield on body length for average seasonal values at Tangalooma (*T*), Byron Bay (*B*), and Carnarvon (*C*) stations (data for first season omitted).

The regressions of average annual oil yield per whale against mean body length of that season's catch, calculated by least squares, differed from one station to another (Fig. 14). Similar slopes of the regressions estimated from catch data at Byron Bay (28° 37′S.) and Tangalooma (27° 11′S.) indicate that these stations differed in only the first two of the five variables listed above as affecting oil yield. Less steeply inclined regressions derived from data collected at whaling stations on the west coast than the regressions from data on the east coast of Australia result from the influence of some factor or factors operating in addition to factory efficiency and sizes of whales killed. The group IV and V populations of humpback whales appear to differ in oil yield to body length relation, quite apart from any differences in factory efficiency or the time and location of commercial operations. There may be a difference in the availability of food to individual humpback whales within Antarctic areas IV and V. At present these possibilities cannot be explored owing to lack of data.

(*c*) *Growth*

Chittleborough (1955*b*) studied the growth of mature female humpback whales taken on the west coast of Australia from 1949 to 1954, using numbers of previous ovulations as an index of age. Although the numbers of ovulations did not give an absolute measure of age, the shape of the growth curve was shown. The data showed that growth ceased at an average length of a little over 45 ft.

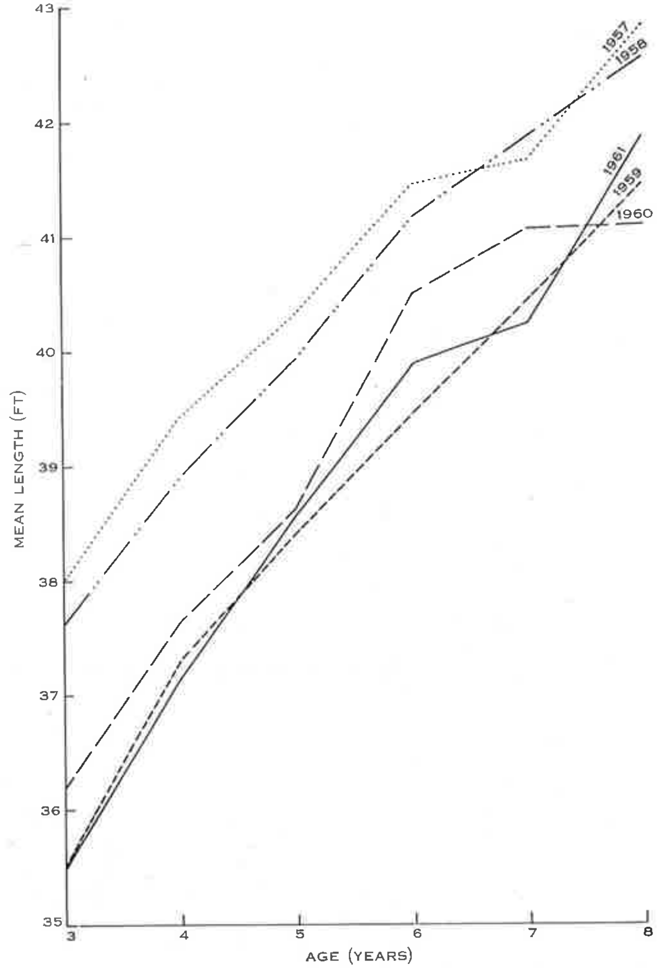

Fig. 15.—Mean lengths of females in age groups 3–8 years sampled off the west coast of Australia, 1957–61; ages from ear plugs.

Chittleborough (1958*b*) gave evidence of an apparent increase in the growth rate of pubertal and young mature females taken on the west coast of Australia in 1956 and 1957, compared with that measured in females of similar ages taken in the period 1949–1954. Although he noted the possibility that this was the result of more stringent selection of large whales by the gunners in 1956 and 1957, Chittleborough suggested that young whales were actually growing faster than previously, as a result of the decrease in numbers of baleen whales competing for food in Antarctic waters.

However, the growth rate (as determined from the age–length relationship in the catch) of young females from the west coast of Australia has apparently decreased since 1957, this being most marked from 1959, as shown in Figures 15 and 16. From the length frequency distribution within age groups 3–6 years (Fig. 16), there was also an apparent decrease from 1960 to 1961 in the growth rate of females sampled by the gunners on the east coast of Australia.

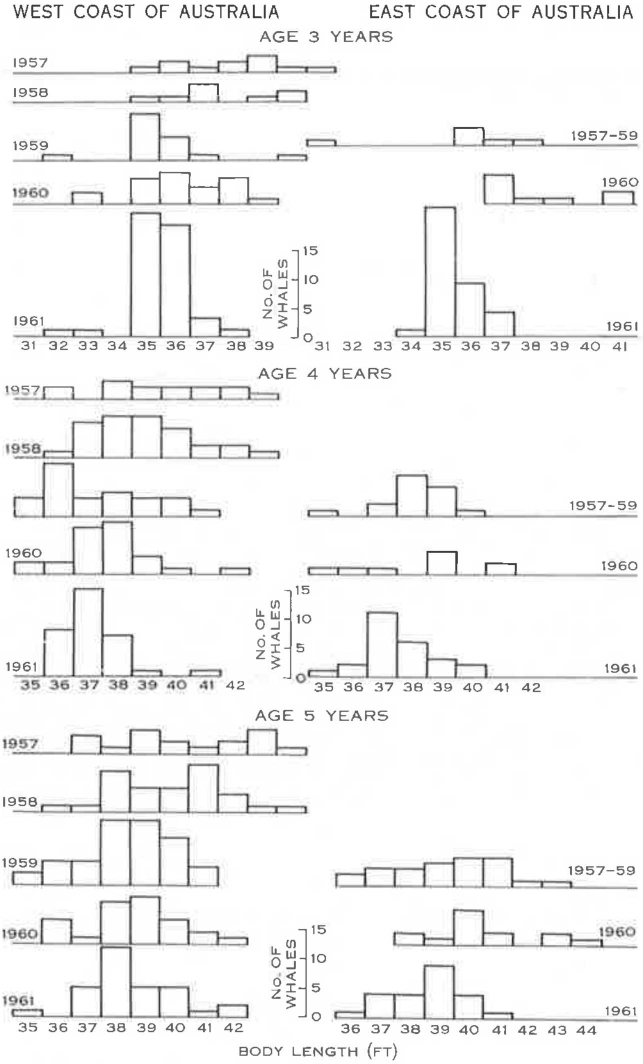

Fig. 16(*a*).—Distribution of lengths in annual samples of females aged 3, 4 anp 5 years (aged from ear plugs).

This appearance of change in growth rates has resulted from changes in the level of selection of the catch by Australian gunners. Chittleborough (1960*b*) has shown that the mean length of pubertal females in annual catches varied with the level of selection applied by gunners in each year. The full series of samples of pubertal females is shown in Table 9. The more careful selection of large whales applied since 1955 following the slight reduction of quotas (see Table 1) resulted in the capture of only the largest (and fastest growing) pubertal females in the following seasons, so that the mean length of pubertal females was higher in 1956 and 1957 than in the period 1949–54. However, as the populations decreased in size, gunners were obliged to take smaller whales, with the result that the mean length of the pubertal females in the catch decreased. The juvenile (immature) section of the population also had been

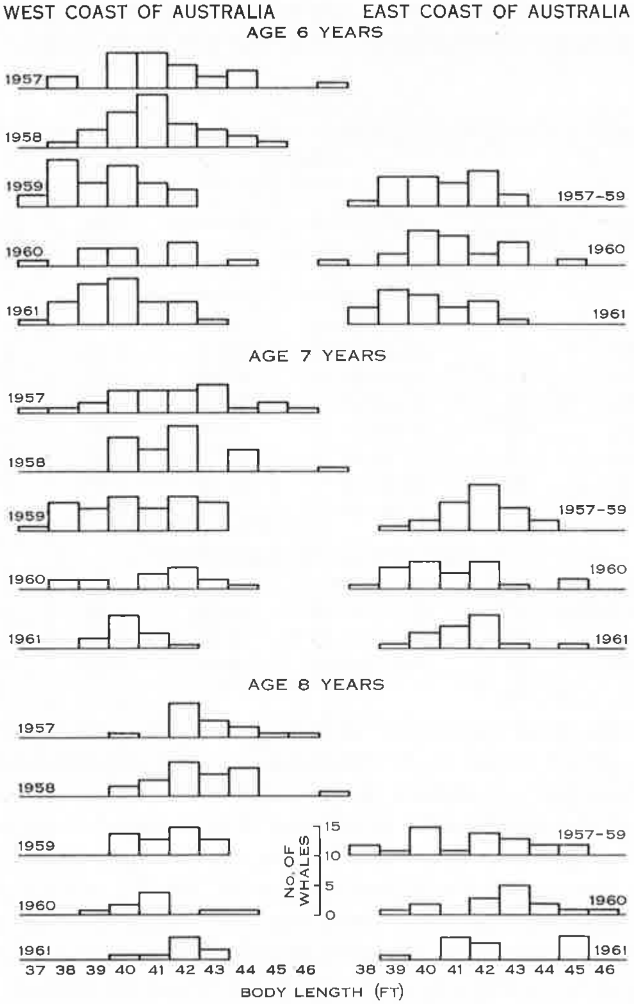

Fig. 16(*b*).—Distribution of lengths in annual samples of females aged 6, 7, and 8 years (aged from ear plugs).

subject to selective hunting, only the largest being killed. Hence, when these young whales reached puberty in following years, the faster growing individuals had already been eliminated so that the mean length of the pubertal females captured was lower than that of the pubertal females of the original (unfished) population of whales.

Table 9 shows that the fall in the level of selection, brought about by the decline of that population, occurred earlier in the case of the group IV than in the group V population.

TABLE 9

LENGTHS OF PUBERTAL FEMALE HUMPBACK WHALES FROM CATCHES ON AUSTRALIAN COASTS

Year	Number Sampled	Range (ft)	Mean (ft)	S.D.	S.E.
		West coast (group IV population)			
1949–54	77	35·25–43·50	38·50	1·66	0·18
1956	17	35·25–45·50	40·15	3·04	0·74
1957	42	35·75–44·50	39·49	2·18	0·34
1958	59	35·00–43·25	39·08	1·11	0·14
1959	43	35·00–40·50	37·96	1·45	0·22
1960	33	35·75–40·50	38·00	1·29	0·23
1961	42	34·50–40·50	37·29	1·43	0·22
1962	44	35·00–40·50	37·75	1·17	0·18
		East coast (group V population)			
1952–54	60	34·50–42·17	38·51	1·73	0·22
1956–59	15	36·33–43·00	39·38	1·81	0·47
1960	11	37·17–40·67	39·21	1·27	0·38
1961	39	35·17–40·50	38·09	1·50	0·24

The evidence given above shows that no growth curve constructed from data on the age and length of whales in the commercial catches will accurately represent the growth of the younger year classes. If the samples obtained in the various years are pooled, some of the errors might cancel out. For example, if the large 6-year-old females taken on the west coast of Australia in 1957 and 1958 (Fig. 16*b*) represented the fast growing section of that population, and the small 6-year-old females taken on the same coast in 1959, 1960, and 1961 represented the slower growing section of that population, then the mean length of the pooled samples from 1957 to 1961 might be close to the true mean length of 6-year-old females in the original population.

While pooling of samples might improve the reliability of the estimated growth curve to some extent, the curve derived from the commercial catches will always be biassed against those age groups whose length range extends below 35 ft (the minimum legal length). This applies to the males below 5 years of age (Table 10, Fig. 17), and to females below 4 years (Table 10, Fig. 18). For these age groups there may be another source of bias in addition to the selection applied by gunners. From time to time some whaling inspectors have recorded lengths of 35 ft or 36 ft (or even more) for small whales which were in fact below the minimum legal length. If the ages of such whales were determined accurately, they would appear in the growth data as unusually large young whales. When there have been few individuals in a particular age group (e.g. at 2 years), the mean length of that age group could be greatly distorted by a few instances of measuring bias.

TABLE 10

LENGTHS* OBSERVED AND ESTIMATED IN EACH AGE GROUP

Determined from ear plugs of 2031 male and 1605 female humpback whales taken on the Australian coast

Age (yr)	Males						Females					
	Observed					Estimated Curve	Observed					Estimated Curve
	Number	Range Min. Length	Range Max. Length	Mean Length	Variance		Number	Range Min. Length	Range Max. Length	Mean Length	Variance	
2	14	32	37	34·86	1·49	34·49	6	32	37	34·33	3·87	34·27
3	149	32	40	35·80	1·51	36·12	151	31	43	36·09	2·95	36·29
4	241	33	41	37·07	1·73	37·43	180	35	43	37·97	2·93	37·94
5	297	35	43	38·65	2·70	38·47	214	35	44	39·11	3·40	39·29
6	281	35	43	39·18	2·22	39·30	190	37	47	40·50	3·02	40·39
7	182	36	44	39·83	2·03	39·97	165	37	47	41·19	3·32	41·28
8	127	37	45	40·44	2·68	40·50	116	38	47	42·10	3·05	42·01
9	128	37	45	40·92	3·02	40·92	88	38	47	42·40	3·37	42·60
10	81	37	46	41·44	3·63	41·25	79	41	46	43·46	2·25	43·08
11	74	38	46	41·68	2·05	41·52	78	38	48	43·23	3·63	43·47
12	62	38	46	41·68	1·26	41·74	54	40	48	43·80	3·60	43·80
13	67	35	45	41·78	2·54	41·91	35	40	47	43·69	2·87	44·06
14	34	39	45	42·06	2·72	42·04	38	40	50	43·47	3·72	44·27
15	28	39	45	41·71	2·49	42·15	36	42	47	44·64	1·95	44·44
16	40	39	45	42·52	1·87	42·24	26	40	48	44·19	4·88	44·59
17	34	39	46	42·56	2·56	42·31	19	43	48	45·42	3·26	44·70
18	23	40	46	42·17	2·04	42·36	21	42	49	44·90	3·59	44·80
19	21	39	46	42·67	2·41	42·41	13	40	47	44·38	3·59	44·87
20	16	38	45	41·69	3·76	42·44	9	44	47	46·00	1·50	44·93
20+	132	39	47	42·64	2·84	L_∞ 42·58	87	42	50	45·46	3·04	L_∞ 45·21

*Lengths in feet.

For the reasons given above, data from males of less than 6 years and from females of less than 5 years were not included in the calculation of the growth curves. The parameters of the growth curves were estimated for the von Bertalanffy growth equation as given by Beverton and Holt (1957), the fitted curves being shown in Figure 19. The form of these curves is:

$$L_t = L_\infty \left[1 - e^{-k(t-t_0)}\right].$$

For the males,

$$L_\infty = 42 \cdot 58 \text{ ft},$$
$$k = 0 \cdot 226,$$
$$t_0 = -5 \cdot 348 \text{ years};$$

and for the females,

$$L_\infty = 45 \cdot 21 \text{ ft},$$
$$k = 0 \cdot 205,$$
$$t_0 = -4 \cdot 936 \text{ years}.$$

The growth curves have been fitted using data from whales ranging from 5 to 19 years of age, and represent the best estimates of growth during these years. Since there are reliable data at certain other points in the life span, the growth curves can be extended to cover most ages.

If the von Bertalanffy curves were extrapolated to age 0 years ($t = 0$), i.e. the time of birth, the mean length of males would then have been 29·87 ft and that of the females 28·78 ft. However, the length of males and females at birth has already been shown to be 14 ft (from measurement of near-term foetuses, which were not subjected to selection or measuring bias).

From the calculated curves the mean length at 1 year of age would be 32·44 ft for males and 31·82 ft for females. The author has examined and measured five small humpback whales identified (from baleen traces and in some cases by the presence of milk in the stomachs) as yearlings, and whose capture was not the result of gunner selection. Two of these yearlings, 28 ft 9 in. and 31 ft 4 in. in length were taken under special licence for research purposes. The other three specimens, 29 ft 3 in., 30 ft 0 in., and 30 ft 3 in. in length, were struck by harpoons intended for their mothers, so that these yearlings might be regarded as random samples of 1-year-old whales. The mean length of these five specimens is 29·92 ft, well below the estimates for the mean length of this age group obtained from the calculated growth curves.

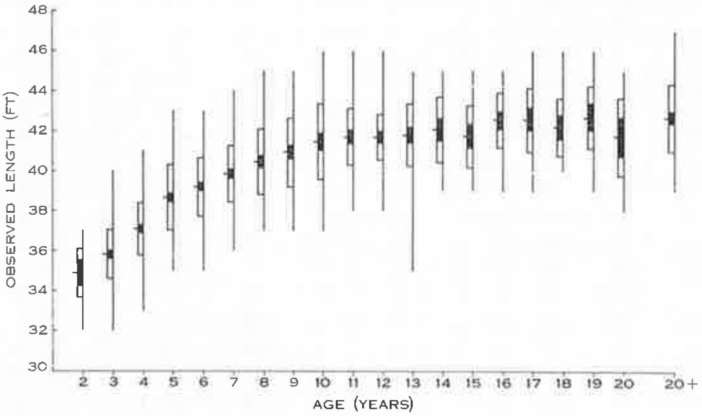

Fig. 17.—Observed lengths within each age group of males. Vertical line shows recorded range; horizontal line gives mean length; black bar extends two standard errors of mean on either side of mean; hollow bar ends one standard deviation on either side of mean. Data from Australian samples aged from ear plugs.

Obviously the slope of the growth curves drawn from data from the commercial catches is not sufficiently steep where it represents the early years of growth. The broken lines in Figure 19 represent more closely the growth during these years.

As shown in Table 10, in both sexes the estimated maximum length, L_∞, is very close to the mean length of individuals over 20 years of age. The length L_∞ is then equivalent to the mean length at physical maturity. The value of L_∞ for each sex, being unaffected by changes in the level of selection, should represent very closely the real values for these populations of whales. The mean lengths of males and females of ages exceeding 20 years in the group IV population did not differ significantly from those in the group V population. There did not appear to be any difference between the two populations under study in respect of rates of growth.

Nishiwaki (1959) gave growth curves (fitted by eye) for humpback whales sampled from catches in the North Pacific Ocean. In his samples the mean length of females at physical maturity was approximately 45·0 ft, while that of the males was close to 43·8 ft. The data do not indicate any real difference in rate of growth of humpback whales in the northern and southern hemispheres.

The largest individual whales of each sex examined by the author were a male of 47 ft, and a female of 51 ft. The latter was not yet physically mature, as the fusion of the posterior vertebral epiphyses had not extended further forwards than the sixth lumbar vertebra, so that this female had not completed its growth.

The oldest humpback whale (based on the examination of ear plugs) examined by the author was 48 years of age (95 ear plug laminations).

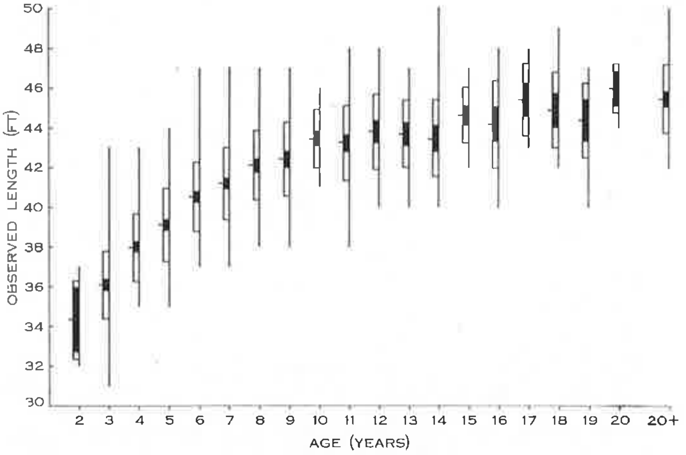

Fig. 18.—Observed lengths within age groups of females sampled at Australian stations. Key as for Figure 17.

IV. History of Exploitation

The group IV population was hunted along the west coast of Australia from 1912 to 1916, from 1925 to 1928, and from 1936 to 1938 (Ruud 1952) and, in the latest cycle, from 1949 to 1963. Insignificant catches were obtained from this population in the Antarctic prior to 1934, but hunting there was intensified from the summer season of 1934–35 to that of 1938–39 (Jonsgård, Ruud, and Øynes 1957).

Ruud indicated that the severely depleted condition of the group IV population in 1938 was caused by the slaughter along the west coast of Australia of 7244 humpback whales from 1936 to 1938. However, the killing of 5429 humpback whales from the same population in the Antarctic from 1934–35 to 1938–39 must also have contributed to the condition of the population in 1938.

From 1935 to 1939 at least 12,673 humpback whales (6804 males and 5869 females) were taken from the group IV population. The catch per unit effort declined towards the end of this period (Ruud 1952) and catching was concentrated upon small whales (see Tables 11 and 12), indicating that the population had been severely depleted.

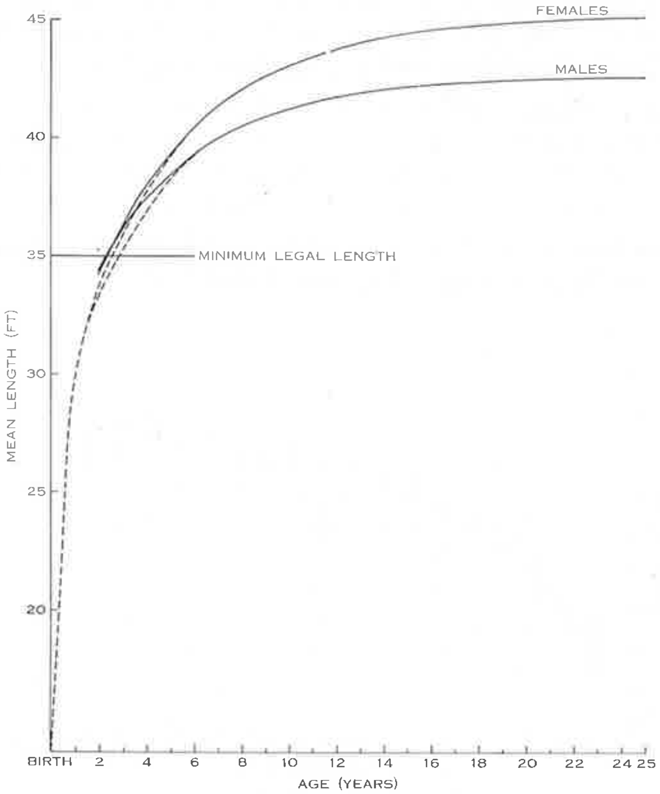

Fig. 19.—Growth curves for group IV and V humpback whales. Solid line estimated from samples of commercial catch; broken line approximate position for natural population.

Individuals of 35 ft in length were highly vulnerable from 1935 to 1939, as shown in Figure 20. Most humpback whales of 35 ft are 3 and 4 years of age (see Section III(*c*)). Therefore, in 1938, humpback whales aged from 3 years and above were greatly reduced in numbers. This means that the year class of 1935, and all earlier year classes, were much reduced by the exploitation of this population from 1935 to 1938. Year classes subsequent to that of 1935 must also have been smaller than year classes in an unfished population, because of the smaller numbers of mature females in the reduced breeding stock.

Humpback whales were fully protected in the Antarctic from 1939 to 1949 except for a temporary relaxation in 1940–41. There was no coastal whaling from Australia during this period.

When commercial operations were re-opened in 1949, the group IV population had apparently recovered in numbers from the depletion induced between 1935 and 1939, but it would still have been deficient in old whales (especially those over 14 years of age) as a result of the operations prior to 1939.

TABLE 11

LENGTH FREQUENCY DISTRIBUTION OF HUMPBACK WHALES TAKEN FROM ANTARCTIC AREA IV, 1934–39

Body Length (ft)	Males						Females					
	1934–35	1935–36	1936–37	1937–38	1938–39	Total Males	1934–35	1935–36	1936–37	1937–38	1938–39	Total Females
24	1					1						
25												
26	1					1						
27	3					3	2		1			3
28	3				1	4	1		2			3
29	2		1		1	4	3			1	1	5
30	6		2	1		9	5		2	1	1	9
31	8		3	1	3	15	2		5	1	3	11
32	18		8	1	1	28	6	1	8	4	7	26
33	18	1	17	2	9	47	9	1	18	1	6	35
34	26	2	22	6	5	61	16		12	4	3	35
35	31	14	43	19	62	169	23	22	37	24	68	174
36	50	17	51	32	30	180	37	32	39	20	33	161
37	46	18	57	22	23	166	26	32	45	23	50	176
38	48	32	48	21	36	185	29	22	43	24	40	158
39	35	34	46	26	7	148	34	34	40	23	21	152
40	73	36	77	45	30	261	55	56	83	53	69	316
41	52	30	60	29	14	185	45	57	45	60	48	255
42	73	22	68	18	11	192	89	50	67	78	59	343
43	47	18	54	18	11	148	66	74	62	78	54	334
44	27	19	44	5	3	98	60	70	63	50	22	265
45	23	9	32	5	6	75	56	92	65	71	54	338
46	15	11	12	2	1	41	51	50	52	36	27	216
47	8	5	14		1	28	37	32	28	32	22	151
48	5	3	3	2		13	33	17	26	15	11	102
49		1	1			2	10	8	12	4		34
50	1					1	10	11	11	8	4	44
51							2	2	5			9
52							2	3	2			7
53							1					1
54												
55												
56												
57	1					1						
Total	621	272	663	255	255	2066	710	666	773	611	603	3363

Catches from this population since 1949 (listed in Table 1) have been limited in various ways. Australian whaling stations have been allotted separate quotas of humpback whales each year by the Australian Government. Catching of humpback whales in the Antarctic (south of 40°S.) was limited to 1250 humpback whales each summer from 1949–50 to 1951–52. This quota applied to the whole of the Antarctic region with the exception of the area from 70°W. to 160°W. which was declared a sanctuary. Since the summer season of 1952–53, limitation of the humpback whale catch has been affected by setting a limit to the time of taking humpback whales (generally a period of 4 days) instead of a direct limit on the number of humpback whales to be taken. The area south of 40°S. from 70°W. to 160°W. remained a sanctuary until the summer of 1955–56. From the summer of 1954–55, waters south of 40°S. between 0° and 70°W. have also been closed to humpback whaling. In 1958–59, the western boundary of this closed sector was changed to 60°W.

TABLE 12

LENGTH FREQUENCY DISTRIBUTION OF HUMPBACK WHALES TAKEN FROM WEST COAST OF AUSTRALIA, 1936–38

Body Length (ft)	Males				Females			
	1936	1937	1938	Total Males	1936	1937	1938	Total Females
24	2			2				
25	4	1		5		1		1
26								
27	1			1	2	2		4
28	3	4	1	8	2	2		4
29	6	1		7	2	1	1	4
30	20	11	1	32	13	16	3	32
31	31	10	4	45	19	9		28
32	41	11	5	57	30	9	3	42
33	49	14	7	70	35	12	5	52
34	52	5	1	58	26	9	1	36
35	217	221	63	501	129	101	40	270
36	151	189	60	400	84	108	33	225
37	135	178	50	363	78	86	29	193
38	215	187	57	459	82	76	28	186
39	188	162	51	401	54	65	28	147
40	280	360	58	698	72	127	31	230
41	246	125	52	423	49	57	34	140
42	191	258	39	488	47	129	41	217
43	153	140	35	328	60	93	40	193
44	85	109	21	215	40	63	35	138
45	45	50	6	101	43	85	21	149
46	18	34	4	56	32	57	15	104
47	5	9		14	15	38	7	60
48	4	1		5	10	18	6	34
49	1			1	5	5	1	11
50					1	2		3
51					1			1
52					2			2
Total	2143	2080	515	4738	933	1171	402	2506

In 1960 the International Whaling Commission proposed to amend the Schedule to the Convention by closing Antarctic area IV (70 °E.–130 °E.) to humpback whaling for a period of 3 years, and reducing the open season for humpback whaling in Antarctic area V (130 °E.–170 °W.) from 4 days to 3 days in each of the following three seasons. However, objections lodged by the governments of Japan, Norway, U.S.S.R., and the United Kingdom (most of the countries engaged in pelagic whaling south of 40 °S.) rendered these amendments ineffective, so that the regulations for humpback whaling in 1960–61 reverted to a 4-day season for the whole of Antarctic waters (south of 40 °S.), with the exception of the area between 0° and 60 °W. which remained closed to humpback whaling.

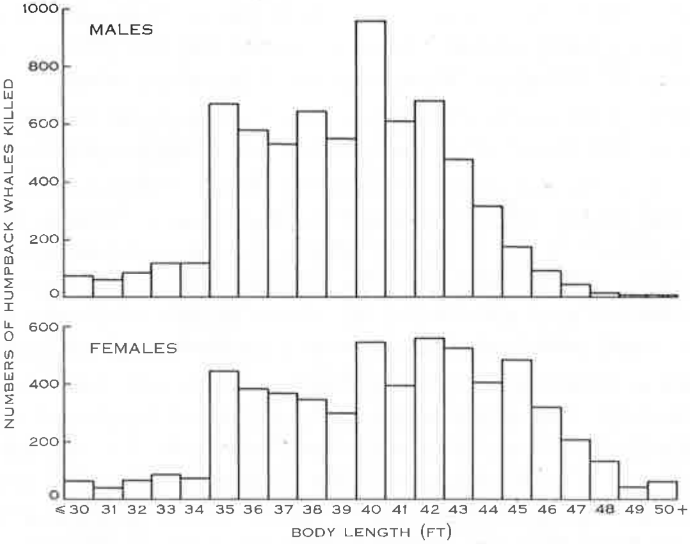

Fig. 20.—Frequency distribution of length in total catch of humpback whales taken from the group IV population, 1935–39.

The group V population was fished only lightly in the years prior to 1950. In the feeding area of this population (130 °E.–170 °W.), 24 humpback whales were recorded in International Whaling Statistics as killed during the summer of 1938–39, and Omura (1953) referred to 201 humpback whales which were killed in this area during the summer of 1940–41. For some years small catches had been taken in New Zealand (Dawbin 1956); and prior to 1930 a few humpback whales were taken at Twofold Bay on the east coast of Australia (Dakin 1934).

Hunting of the group V population was re-opened in the Antarctic in 1949–50, and on the east coast of Australia in 1952, as shown in Table 2. Catch limits in these localities have been the same as those described above for the corresponding regions of the group IV population.

V. Population Structure

(*a*) *Sex Ratio*

Chittleborough (1958*c*) recorded 51·9% males amongst 1448 humpback whale foetuses taken during mid-pregnancy from Antarctic areas IV and V. At Australian whaling stations, 615 near-term foetuses have been recorded in the catches from 1949 to 1962; 52·2% of these were males. As foetuses are not subject to the sampling bias which is found in most commercial catches, the sex ratio at birth may be taken to be inclined towards males.

The sex ratio within the juvenile and adult portions of the population is less easily determined, because of varying kinds and intensity of selection applied in commercial whaling. Matthews (1938) has shown that females predominate in Antarctic (area II) catches, while males are in excess of females in catches from temperate waters (South Africa). Table 13 shows that this also occurs in catches from the group IV and group V populations of humpback whales.

The cause of the excess of females in Antarctic catches is obscure. There is no evidence of any segregation of the sexes during the summer feeding period.

The reasons for the excess of males in most catches from temperate and tropical regions are less obscure. Some 37% of the mature females give birth each year (Section III(*a*)(iv)), and pregnant females are late in the northward migration (Section II(*d*)(ii)), giving birth soon after reaching temperate waters, so that in subtropical waters at least one-third of the mature females are protected. Catches in warm waters would then be expected to have a preponderance of males.

The area in which chasers from the whaling station near Albany (Western Australia) operate is one of the few in which mature males and females are equally vulnerable, pregnant females being killed when they first reach 35°S. latitude, and before parturition occurs. The relative abundance of mature males and females can be measured by the catch per unit effort within weekly periods throughout the northward migration past this station (Table 7). From these data, the ratio of abundance of mature males to mature females for the whole of the northward migration was 5·17 : 4·71 or 52·3% males. This is in close agreement with the percentage of males at birth.

Table 13 shows that on both the west and east coasts of Australia, the percentage of males in the annual catch tended to decrease in successive years. Budker (1953) showed a similar trend within catches off the coast of Gabon, the percentages of males killed being:

Year	Total Catch	Males (%)
1949	1356	64·6
1950	1404	57·6
1951	1105	49·1
1952	246	41·6

Because of differences in the times of migration of various categories (Section II (*d*)(ii)), the sex ratio within the catches will change as the humpback migratory stream moves past the shore stations. Thus, a change in the sex ratio of the total catch from one year to another could be caused by the whaling operations having taken place over different periods of the 2 years. However, Chittleborough (1960*a*, Fig. 10) showed that when the same (weekly) periods at the same locality are compared, there has been a regular increase in the percentage of females in the catches of recent years.

TABLE 13

PERCENTAGES OF MALES IN CATCHES FROM THE GROUP IV AND V POPULATIONS OF HUMPBACK WHALES

Year	Total Catch	Number of Males	Percentage of Males	Year	Total Catch	Number of Males	Percentage of Males
	West coast of Australia				*Antarctic area IV*		
1935	0	0	—	1935	1331	621	46·7
1936	3076	2143	69·7	1936	938	272	29·0
1937	3251	2080	64·0	1937	1436	663	46·2
1938	917	515	56·2	1938	866	255	29·4
1939	0	0	—	1939	858	255	29·7
Total	7244	4738	65·4	Total	5429	2066	38·1
1949	190	135	71·1	1949	0	0	—
1950	387	250	64·6	1950	779	354	45·4
1951	1217	907	74·5	1951	1112	468	42·1
1952	1182	666	56·3	1952	1127	546	48·4
1953	1297	726	56·0	1953	193	103	53·4
1954	1309	692	52·9	1954	258	133	51·6
1955	1123	580	51·6	1955	28	12	42·9
1956	1119	676	60·4	1956	824	320	38·8
1957	1119	583	52·1	1957	0	0	—
1958	967	509	52·6	1958	0	0	—
1959	700	331	47·3	1959	1413	645	45·6
1960	545	271	49·7	1960	66	28	42·4
1961	578	306	52·9	1961	4	3	
1962	543	304	56·0	1962	56	24	42·9
Total	12,276	6936	56·5	Total	5860	2636	45·0
	East coast of Australia				*Antarctic area V*		
1950	0	0	—	1950	903	441	48·8
1951	0	0	—	1951	162	79	48·8
1952	598	448	74·9	1952	146	51	34·9
1952	700	509	72·7	1953	504	212	42·1
1954	718	511	71·2	1954	0	0	—
1955	720	494	68·6	1955	1097	457	41·7
1956	720	485	67·4	1956	194	91	46·9
1957	721	492	68·2	1957	0	0	—
1958	720	511	71·0	1958	0	0	—
1959	810	543	67·0	1959	885	458	51·8
1960	810	496	61·2	1960	931	407	43·7
1961	731	448	61·3	1961	293	135	46·1
1962	177	103	58·2	1962	0	0	—
Total	7425	5040	67·9	Total	5115	2331	45·6

The decline in the percentage of males in the catch is linked with the rate of exploitation of the population in lower latitudes. Intensive fishing in warm waters reduces the male portion of the population faster than the female portion. This effect is even greater over the range of mature individuals because commercial catches initially contain more immature females than immature males (see Section V(*d*)). Since the stock of mature males is reduced faster than that of the mature females, the percentage of males in the total catch decreases from year to year. This trend can occur only when the greater part of the total catch is taken from lower latitudes (temperate and subtropical waters), rather than from Antarctic waters.

Of the total overall catch of humpback whales from the whole of the group IV population from 1949 to 1962, 52·8% of the 18,136 humpback whales killed were males. This is very close to the percentage of males at birth and the estimate of the percentage of males in the stock of adults passing Albany during the northward migration.

(*b*) *Size Composition*

(i) *Relation between Size Composition of Catch and of Population*

As stressed in Section I (*b*) (i), commercial catches of whales may be far from random samples of the populations from which they were drawn. The size composition of a particular catch depends on the following factors:

(1) Rate of growth of individuals;

(2) Natural mortality;

(3) Time and place of sampling;

(4) Level of selection by gunners;

(5) Effects of previous hunting (fishing mortality).

There is no evidence that either the first or second of these has changed appreciably during recent years, and variations in the time and place of sampling have had only slight effect upon the size composition of catches. Changes in the size composition of the catches have therefore been the result primarily of variations in the level of selection by gunners and the effects of previous fishing mortality.

The level of selection by gunners has not been simply the observation of the minimum legal length of 35 ft. Selection (by size) has varied from one gunner to another, from one whaling station to another, and from one time to another. Selectivity has been influenced greatly by the type of incentive payments made to gunners. Bonuses based upon numbers of whales killed tend to discourage selection, because under those conditions gunners take whatever appears to be safely over 35 ft in length. On the other hand, bonuses based on oil yield or directly upon the length of each whale, lead gunners to look for bigger whales. Chittleborough (1960*b*) has shown that the mean length of pubertal females taken each year on the Australian coast has varied with the degree of selection applied by gunners and has also been influenced by previous selective killing of a diminishing stock.

In the Antarctic, limitation of the pelagic catch by limiting either the period of open season, or the total number of whales to be caught, had resulted in strong competition between the various expeditions for the highest proportion of the overall catch, so that selection there was at a minimum.

(ii) *Catches from the Group IV Humpback Whale Population*

The size composition of the catches recorded from the group IV population of humpback whales from 1949 to 1962 is shown in Tables 14–17. The majority of these data are from catch returns forwarded to the Bureau of International Whaling Statistics in Sandefjord, Norway. The data for Antarctic catches of 1959 have been adjusted in accordance with the evidence (Chittleborough 1959*b*) of intermingling of the group IV and V populations of humpback whales in the eastern portion of Antarctic area IV during the summer of 1958–59.

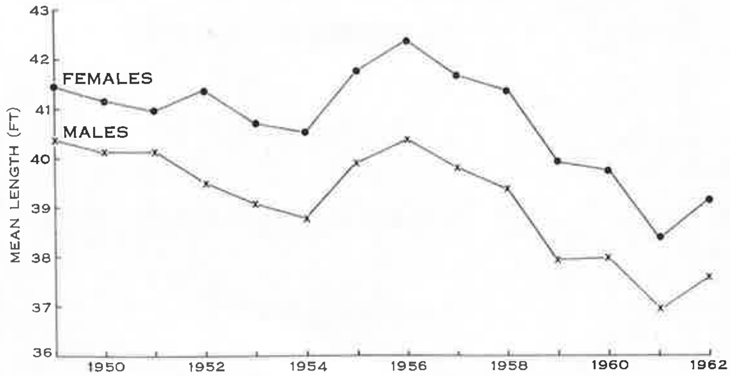

Fig. 21.—Mean lengths of annual catches of male and female humpback whales from the west coast of Australia, 1949–62.

There was little change in selectivity on the west coast of Australia from 1949 to 1954, but the mean lengths of both males and females in the catch declined during this period (Tables 14 and 15, Fig. 21). Mature males were more heavily fished than the mature females, with the result that the mean length of the males decreased more rapidly than that of the females.

Reduction of quotas prior to the 1955 whaling season (Table 1) stimulated more careful selection of large whales. At one station on the west coast the gunners were instructed to shoot, where possible, only those whales that appeared to be 40 ft or more in length, while another station introduced a new bonus system whereby the catchers were paid a bonus for every whale exceeding the average length in the previous season of 39·58 ft.

With the closing of one station on the west coast in 1956 (Table 1) and the concentration of catching power at Carnarvon, the level of selection was raised still higher, and the mean lengths of males and females in the catch rose to maxima in that year (Fig. 21). The increased selection from 1954 to 1956 caused the mean length of the females to rise more than that of the more heavily fished males.

Although attempts were made to maintain a high degree of selection after 1956, large whales became less abundant each year, so that gunners were obliged to accept

TABLE 14

GROUP IV POPULATION OF HUMPBACK WHALES

Distribution of lengths within catches from the west coast of Australia—Males

Length (ft)	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
30				1		1							1	
31		1												
32		2		1	4					1			2	2
33			5	3	4			2			4	4	3	1
34				5	1		1		4	2	3	3	6	1
35	1	5	17	38	49	46	16	11	13	20	24	14	56	28
36	3	10	38	36	62	72	27	28	28	27	46	27	51	46
37	11	15	64	71	84	87	35	30	40	48	59	54	58	79
38	18	16	81	72	112	127	60	55	77	68	70	62	59	53
39	23	38	133	106	111	113	98	78	98	82	57	50	41	46
40	16	51	167	97	96	84	133	131	102	102	35	25	18	25
41	20	41	167	88	66	61	63	114	69	64	15	18	6	15
42	20	41	108	66	68	51	69	102	71	47	8	7	3	5
43	12	17	72	52	28	23	42	72	38	29	2	5	1	3
44	6	8	37	18	21	18	19	29	27	10	3	2	1	
45	4	4	15	8	16	6	12	18	13	6	3			
46	1	1	3	3	4	3	4	2	3	2	1			
47				1			1	3		1	1			
48								1						
Total	135	250	907	666	726	692	580	676	583	509	331	271	306	304
Mean length (ft)	40·36	40·10	40·11	39·48	39·05	38·77	39·88	40·35	39·78	39·35	37·93	37·97	36·96	37·60

Table 15

GROUP IV POPULATION OF HUMPBACK WHALES

Distribution of lengths within catches from the west coast of Australia—Females

Length (ft)	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
29				1	1		2							
30				1	2									
31				1	2		1							
32	1	1			1	1		1			1	1	1	
33	1		1	1		3	2	1			2	3	6	3
34		1	1						1	1	2	1		1
35	1	4	12	17	36	42	7	6	2	10	26	12	34	17
36	3	9	9	27	33	48	13	11	18	10	30	24	39	19
37	1	8	25	31	41	46	20	7	26	17	22	28	35	42
38	4	7	26	21	58	62	38	13	28	30	42	42	35	43
39	5	10	27	43	51	53	48	33	56	47	35	24	31	27
40	1	16	38	48	47	63	70	58	59	64	55	25	28	21
41	5	12	33	61	53	42	54	37	55	52	46	27	13	26
42	12	21	36	62	55	53	58	48	63	53	30	28	19	12
43	6	15	38	62	52	61	60	53	77	61	24	23	12	6
44	5	9	29	53	57	57	55	68	55	45	16	12	9	10
45	6	11	17	36	27	33	39	43	34	29	19	10	7	7
46	2	9	10	27	29	32	39	26	39	20	10	5	1	3
47	1	2	4	14	17	9	23	20	17	11	4	6	1	
48		2	2	7	8	7	9	10	5	8	5	1	1	
49	1		1	1	1	3	3	7	1			2		1
50			1	2		1	2	1						1
51														
52						1								
Total	55	137	310	516	571	617	543	443	536	458	369	274	272	239
Mean length (ft)	41·43	41·15	40·92	41·35	40·67	40·50	41·72	42·32	41·62	41·33	39·88	39·73	38·35	39·18

smaller whales, with the result that the mean lengths of males and females in the catch progressively declined, as shown in Figure 21.

In 1961 selectivity was changed again by a variation in whaling tactics. At the larger of the two remaining humpback whaling stations on the west coast of Australia (i.e. that at Carnarvon) the bonus system, previously based on the sizes of whales captured, reverted to one based on numbers captured. This stimulated the rate of capture of whales, and selection of large individuals was abandoned, so that the mean lengths of catches fell to the lowest level in 13 years (Fig. 21), catches being concentrated upon whales at or very close to the minimum legal length (Tables 14 and 15).

TABLE 16

GROUP IV POPULATION OF HUMPBACK WHALES

Distribution of lengths within catches from the Antarctic — Males

Length (ft)	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
28			2										
29													
30	2	3	2	1						4			
31		1	1				1						
32	2	5	7	1		1				5			
33	4	10	13	5		1				1			
34	8	4	2				1			4			
35	19	11	68	10	11	1	14			74	6		2
36	31	38	46	12	9	1	35			84	3		2
37	34	57	40	14	19	1	53			105	3		2
38	22	40	43	19	24	1	48			116	4		3
39	36	55	63	13	24	1	42			94	6		2
40	58	62	74	9	19	2	58			65	3		8
41	40	60	62	5	8	1	34			47	2		2
42	46	56	52	6	11	1	16			33			3
43	25	33	28	4	3	1	8			8	1		
44	16	15	21	2	3		8			4			
45	8	17	13	1			2			1		1	
46	2		5		1								
47	1	1	3	1	1							1	
48												1	
49			1										
Total	354	468	546	103	133	12*	320	0	0	645*	28	3	24
Mean length (ft)	39·48	39·44	39·00	38·11	38·83		38·78			37·98			

*After adjustment of numbers reported to International Whaling Statistics.

Because of the numbers of small humpback whales very close to the minimum legal length taken in 1961, the Australian companies were reminded prior to the 1962 humpback whaling season that the minimum legal length would be enforced strictly.

The mean length of males and females captured on the west coast in 1962 increased slightly from the values of the previous year (Fig. 21). This was achieved by sparing slightly higher proportions of individuals close to the minimum legal length; in other respects the length frequency distribution of the catches in 1962 was similar to that of 1961 (Tables 14 and 15).

TABLE 17

GROUP IV POPULATION OF HUMPBACK WHALES

Distribution of lengths within catches from the Antarctic — Females

Length (ft)	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
27			2										
28										1			
29	2	1	1							1			
30	1	1	1		2					3			
31		1	5				1			6			
32	4	5	4		1		2			6			
33	6	9	8	3		1				1	1		
34	3	4	3			1							
35	11	15	52	7	11	1	15			68	6		1
36	13	26	32	3	5	1	43			70	3		2
37	18	28	24	7	11	1	37			55	1		4
38	27	50	29	10	18	1	40			75	1		5
39	38	47	48	8	13	1	46			80	4		2
40	45	48	58	9	18	2	63			91	2		3
41	36	69	52	10	12	1	65			80	2		1
42	62	97	54	13	9	2	60			74	1		8
43	47	79	54	5	8	1	39			52	3		3
44	49	71	43	3	5	1	38			42	7		2
45	32	35	40	4	4	1	24			30	2		
46	15	28	37	3	5	1	23			20			1
47	11	18	18	1			7			7	1		
48	4	10	10	4	2		1			3	3		
49	1	2	2										
50			2		1					3	1	1	
51			2										
Total	425	644	581	90	125	16*	504	0	0	768*	38	1	32
Mean length (ft)	41·15	41·22	40·72	40·26	39·72		40·52			39·67			

* After adjustment of numbers reported to International Whaling Statistics.

(iii) *Catches from the Group V Humpback Whale Population*

The size composition of the catches recorded from the group V population of humpback whales from 1949 to 1962 is shown in Tables 18–24. These records are from catch returns forwarded to the Bureau of International Whaling Statistics, with the exception that the data for Antarctic catches of 1955 (the summer of 1954–55) include the original records from the factory ship *Olympic Challenger*, instead of the amended returns supplied by that expedition to the Bureau of International Whaling Statistics.

The data for Antarctic catches of 1959 have been adjusted in accordance with the evidence of intermingling of the group IV and group V populations in that summer, as already discussed.

The size composition of catches taken on the east coast of Australia reflected changes in selectivity induced mainly by events on the west coast. Although the size composition of the catches on the east coast had not changed appreciably from 1952 to 1954, the slight reduction of quotas on the west coast prior to the 1955 whaling season, caused more stringent selection of large whales to be applied on the east coast from that year onwards. The mean lengths of both males and females in the catches increased in 1955 and remained high until 1959 (Fig. 22). The mean length of males and females decreased slightly from 1959 to 1960, and in the following years fell drastically (Fig. 22), the mean length of the females taken on the east coast in 1962 being less than that of the females taken on the west coast of Australia in the same year (Tables 19 and 15, respectively).

TABLE 18

GROUP V POPULATION OF HUMPBACK WHALES

Distribution of lengths within catches from the east coast of Australia — Males

Length (ft)	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
30			1		1						1
31	1	1									1
32	1		1		1					3	
33	1		1	2	2	2			2	1	1
34	1	2		1			1		1	2	
35	6	9	18	10	7	5	6	6	7	47	15
36	15	9	13	13	11	14	8	11	12	41	14
37	20	31	18	21	22	20	18	14	26	46	15
38	42	50	59	32	25	46	31	42	46	59	10
39	65	75	75	55	56	57	45	50	63	50	9
40	77	76	89	92	97	94	76	82	78	51	11
41	86	94	78	79	82	88	114	96	84	47	10
42	71	89	78	82	81	96	84	93	66	51	7
43	40	56	47	66	51	40	75	81	62	25	5
44	15	14	19	30	27	23	26	43	31	13	1
45	6	3	11	7	15	3	15	18	9	8	
46	1		3	3	6	4	12	6	5	3	
47				1				1	3	1	
48					1				1		
Total No.	448	509	511	494	485	492	511	543	496	448	100
Mean length (ft)	40·25	40·25	40·17	40·59	40·65	40·38	40·96	41·00	40·47	39·06	38·03

The small catches taken off Norfolk I. were generally composed of humpback whales larger than those in the catches from other localities within this population (compare Table 20 with Tables 18, 19, and 21–24). This has been due mainly to the very stringent selection of large whales successfully applied by the small station at Norfolk I., rather than to real differences in the size composition of the whales passing the various sampling points.

In the decline in size composition of catches from the two populations the mean length of the males from the group IV population decreased more rapidly than that of the females, whereas in the group V population the mean length of the females decreased far more rapidly than that of the males. These differences resulted from higher fishing mortality in males than in females of the group IV population, and the reverse in the case of the group V population, as discussed in Section VII.

TABLE 19

GROUP V POPULATION OF HUMPBACK WHALES

Distribution of lengths within catches from the east coast of Australia — Females

Length (ft)	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
31						1	1				
32	1	2	3							3	
33		2	4		1		1	1	1	2	1
34		1			1	1	1		2	4	6
35	5	7	9	7	3	7	1	1	4	38	5
36	5	11	4	3	4	7	3	6	3	21	12
37	11	7	6	12	15	13	5	11	15	28	6
38	6	11	20	13	10	17	14	15	11	32	8
39	15	21	28	21	11	16	12	19	25	33	4
40	14	11	16	27	22	14	18	15	35	23	11
41	20	29	31	22	23	29	22	29	38	24	3
42	22	34	24	27	30	33	30	33	43	25	6
43	21	32	19	27	42	24	26	36	43	12	4
44	14	12	17	23	34	27	22	41	27	7	3
45	10	5	8	22	20	18	26	26	28	18	2
46	1	1	12	9	9	12	15	18	20	5	1
47	4	3	5	9	8	4	7	13	12	3	1
48			1	3	2	4	4	2	3	4	
49		1				1	1		2	1	
50		1				1		1	2		
51				1							
52	1										
Total No.	150	191	207	226	235	229	209	267	314	283	73
Mean length (ft)	41·06	40·66	40·74	41·66	41·85	41·47	42·15	42·22	41·88	39·22	38·64

The maintenance of the size composition of catches from the east coast up to 1959, contrasted with the declining sizes of whales taken on the west coast during the same period (Figs. 22 and 21, respectively), is further evidence of the lack of regular exchange between these two populations of humpback whales, as discussed in Section II(*b*).

(*c*) *Age Composition*

Ages were determined from collections of ear plugs and ovaries obtained from catches at Australian Whaling stations. Two laminations in the ear plugs were taken as representing 1 year, as shown by Chittleborough (1959*c*) and later verified by the evidence from two marked whales (Chittleborough 1960*c*, 1962). Age was estimated from the ovaries by dividing the total number of previous ovulations by 1·1 (the average annual rate of ovulation), and adding 5 years for the age at maturity (Chittleborough 1959*c*).

TABLE 20

DISTRIBUTION OF LENGTHS IN CATCHES AT NORFOLK I.

Length (ft)	Males							Females						
	1956	1957	1958	1959	1960	1961	1962	1956	1957	1958	1959	1960	1961	1962
30				1										
31														
32												2		
33			1									1		
34						2								
35	2	2		4		2		4				2	2	
36	4	1	1	4	1	2		1		1	3		4	
37	4	5	1	4	8	6		4	2	1	2	1	4	
38	3	4	2	8	9	8	1	3	2			1	5	
39	6	3	4	13	12	10		3		2	1	6	2	
40	8	14	11	15	15	18		6	2	4	3	7	2	
41	16	15	12	18	17	23	1	4	2	5	3	11	1	
42	17	19	12	13	21	23		5	5	5	4	7	8	
43	15	18	10	3	6	18		5	4	6	7	9	4	
44	11	7	5	4	3	5		4	1	10	12	9	3	
45	3	4	3	3	4	6	1	4	4	10	9	8	4	
46	2					1		6	4	6	11	5	1	
47	1	1	1					4		6	1	4	2	1
48								5	1	1	3	1	2	
49											1			
50													2	
Total catch	92	93	63	90	96	124	3	58	27	57	60	74	46	1
Mean length (ft)	41·31	41·24	41·35	40·75	40·48	40·85		42·09	42·47	43·40	43·47	42·10	41·46	

The sizes of these age samples in relation to the catches are shown in Table 3. Ear plugs were collected only from 1956 onwards. Collections of ovaries were always larger than those of ear plugs obtained from females.

Although the larger collections obtained in recent years may be taken as direct measures of the age composition of the corresponding commercial catches (Chittleborough 1962), the best estimate of the age distribution within the catch is obtained by applying the age–length key derived from the age sample to the length frequency distribution of the commercial catch (as discussed in Section I(*b*)(i)).

For a catch from which the age sample was small or not obtained, the most suitable age–length key should be applied to the length frequency distribution of that catch. Some care is required in the choice of the age–length key most applicable in such instances, because the age–length relation has been shown to vary from one catch to another from the same population as detailed in Section III(*c*). Selection of large whales may take the older whales almost at random, but from each of the younger age groups will take only the largest individuals. When most of the large whales have been removed by prolonged selective killing, only small individuals remain to be taken from the younger age groups. The few large whales in the catches will then be relatively young (fast growing) individuals which had escaped the catches for a time.

TABLE 21

GROUP V POPULATION OF HUMPBACK WHALES

Distribution of lengths within catches from New Zealand, 1949–62—Males*

Body Length (ft)	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
34			1	6		2		1	2	1		1		1
35	5	1	6	4	7	14	5	6	6	9	8	11	3	2
36	3	3	7	1	5	7	5	8	9	4	18	32	5	4
37	8	2	3	5	1	5	7	8	13	11	14	26	4	2
38	7	1	7	1	1	5	5	3	5	13	23	26	3	4
39	10	6	5	6	5	10	2	6	9	10	15	20	1	2
40	13	8	7	10	8	12	11	7	14	12	23	23	5	
41	9	11	8	11	3	16	6	12	14	10	24	27	10	2
42	15	7	9	8	8	12	8	7	9	18	24	17	4	1
43	2	9	8	8	12	6	8	9	13	7	9	20	8	3
44	9	2	5	5	6	6	6	4	4	10	16	13	4	1
45	4	2	3	6	3	4	4	5	2	4	5	7	3	
46	2		2		3	2	2		1	1	1	1		1
47	2		1		1	1		3	1	1	1	2		
48					2		2	1		1		1		
49				1										
50				1		1								
Total	89	52	72	73	65	103	71	80	102	112	181	227	50	23
Mean length (ft)	40·47	40·75	40·17	40·51	41·08	39·86	40·56	40·24	39·75	40·11	39·92	39·55	40·38	38·91

* Data from International Whaling Statistics.

In estimating the age composition of the catches of males, the age–length key from each age sample was applied to the length frequency distribution of the corresponding catch, for each of the annual catches of males from the west coast from 1957 to 1962 (Table 25), and from the east coast in 1957, and from 1959 to 1962 (Table 26). For the catch of males taken on the east coast in 1958, a combined age–length key for all males aged on the east coast from 1957 to 1961 was applied to the length frequency distribution of the 1958 catch.

The size composition of catches of males from the east coast was fairly constant from 1952 to 1960 (Fig. 22) and there was little evidence of change in the age–length relation in collections of ear plugs obtained from 1957 to 1961. Therefore, a single age–length key, prepared from all males aged on the east coast from 1957 to 1961, was applied to the length frequency distribution of the east coast catches of males in each year from 1952 to 1956, to establish the age composition within catches of east coast males of those years.

TABLE 22

GROUP V POPULATION OF HUMPBACK WHALES

Distribution of lengths within catches from New Zealand, 1949–62—Females*

Body Length (ft)	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
33				1										
34				3	1	2	1		1					
35		3	2	6	6	6	2	7	8	2	7	6		
36	3		1	6	5	10	5	5	1	10	14	9	2	2
37	3	4	1	1	2	3	4	4	9	7	16	9	4	
38	4		2	3		5	2	5	2	1	8	16	6	1
39	5	1	8	1	2	3	1	6	7	3	10	9	3	3
40	6	2	3	2		7	7	1	4	3	10	12		1
41	7	4	3	2	4	7	1	6	9	6	10	12	1	1
42	5	3	5	7	2	7	7	3	6	5	5	16	3	
43	3	3	5	5	5	7	3	2	7	9	14	7	4	
44	4	2	4	3	3	4	1	8	11	8	13	9	5	
45	9	2	3	2	4	2	3	6	4	7	14	13		
46		2	1	3	3	6	1	6	6	6	8	12	1	
47				1	3	3		1	2	1	5	1		1
48		1		2	2	2	2	2	2	3	1	1	1	
49	2				2	3	1	1	1		2	2		
50			1											
51	1													
Total	52	27	39	48	44	77	41	63	80	71	137	134	30	9
Mean length (ft)	41·58	41·07	41·18	40·10	41·45	40·83	40·51	41·03	41·16	41·42	40·93	41·02	40·60	39·44

* Data from International Whaling Statistics.

Catches of males from the east coast from 1957 to 1961 appeared to be from a stock still containing a greater accumulation of old males than found in catches of the same years from the west coast of Australia (Chittleborough 1962). The lengths of the males taken on the west coast in earlier years (1949–1956) were generally greater than those of more recent years (Table 14). In the earlier years the group IV population probably contained an accumulation of old whales, although because of its previous history of exploitation (Section IV), the group IV population would not have contained, in the 1950's, as great an accumulation of old whales as the group V population.

The size composition of the catches of males from the west coast in the early 1950's was intermediate between the size composition of aged samples of males taken on the west and east coasts from 1957 to 1961 (Fig. 23). The age composition of catches of males from the west coast each year from 1949 to 1956 was estimated by applying to the length frequency distribution of each of these years a pooled age–length key obtained from all males aged on the west and east coasts in the period 1957 to 1961 (Table 25).

TABLE 23

GROUP V POPULATION OF HUMPBACK WHALES

Distribution of lengths within catches from the Antarctic — Males*

Length (ft)	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
23						3							
24						1							
25	3												
26						5							
27						4							
28						6							
29			1			3							
30	1	1				14					1		
31						8							
32	5			1		22							
33	7	1		3		26					1	1	
34	3			1		14	4			1	4		
35	16	1	6	4		34	2			11	21	3	
36	20	1	3	12		38	6			24	32	5	
37	27	4	3	18		29	8			32	40	9	
38	26	6	3	20		45	17			34	44	25	
39	55	3	1	20		48	20			67	53	27	
40	73	12	8	31		63	18			70	46	19	
41	60	15	10	24		17	6			53	55	9	
42	62	15	4	39		31	4			82	43	11	
43	38	6	3	11		20	3			55	33	4	
44	21	8	4	15		11	2			17	17	14	
45	17	5	5	8		7	1			8	9	4	
46	3			2		4				3	3	3	
47	4	1		1		3				1	3	1	
48				1		1							
49													
50				1							1		
51													
53											1		
Total	441	79	51	212	0	457*	91	0	0	458†	407	135	0
Mean length (ft)	40·01	40·94	39·98	40·26		37·32	38·90			40·28	39·71	39·99	

* From original records of F.F. *Olympic Challenger*.

† Adjusted values.

The age composition of catches of males at Norfolk I. was determined by applying an age–length key obtained from ear plugs collected there from 1957 to 1961, to the length frequency distribution of each year's catch, with the results shown in Table 27.

TABLE 24

GROUP V POPULATION OF HUMPBACK WHALES

Distribution of lengths within catches from the Antarctic — Females

Length (ft)	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
25						1							
26						3							
27						2							
28	1					3							
29						4							
30	1			1		10							
31	6					3					1		
32	5		1			16					1		
33	6			1		21					1	1	
34	3					19	1				4	2	
35	19	1	5	11		35	2			4	10	1	
36	17	1	2	11		27	8			19	25	2	
37	11	1	4	13		22	13			26	32	7	
38	33	2	4	10		39	12			21	37	17	
39	26	2	2	13		33	13			55	48	19	
40	48	8	3	29		78	15			41	56	18	
41	54	8	7	17		59	11			57	47	12	
42	61	11	11	48		84	5			53	49	17	
43	57	7	13	32		60	10			64	45	16	
44	50	18	12	32		53	5			30	57	12	
45	28	10	15	32		38	5			28	34	8	
46	20	9	8	22		19	1			17	35	6	
47	11	2	4	10		8	2			8	17	10	
48	5	2	3	5		3				2	9	3	
49		1	1	3						2	9	5	
50				2							2	1	
51											5	1	
Total	462	83	95	292	0	640*	103	0	0	427†	524	158	0
Mean length (ft)	41·00	42·99	42·49	42·01		39·79	39·92			41·26	41·56	41·72	

* From original records of F.F. *Olympic Challenger*.

† Adjusted values.

In the case of the females, ovaries were used for assessing the age composition of catches, since the samples of ovaries were far larger than those of ear plugs. An age–length key based on ovarian data does not separate immature and pubertal females (ovary group "O") into age groups: this was done by means of collections of ear plugs from immature and pubertal females.

From the discussion of selectivity in Sections I(*b*)(*i*) and V(*b*), the sequence of recent whaling on the west coast of Australia can be divided into three broad periods.

From 1949 to 1954 selection was at a low level; from 1955 to 1958 selection was high and effective; while from 1959 to 1962 selection was ineffective as the large whales had been removed from the population. An age–length key was prepared from the ovarian data collected on the west coast in each of these periods, and applied to the length frequency distribution of the annual catches within the respective periods, with the results shown in Table 28.

There have also been changes in selection of catch on the east coast of Australia, but not of quite the same magnitude, and though there has been a shift in the sizes and ages of whales taken, this has not resulted in a significant change in the age–length relation. Hence, the age composition of each year's catch of females from the east coast was determined by applying the length frequency distribution of that year's catch to a pooled age–length key containing all the ovarian data collected on that coast from 1952 to 1962, with the results shown in Table 29.

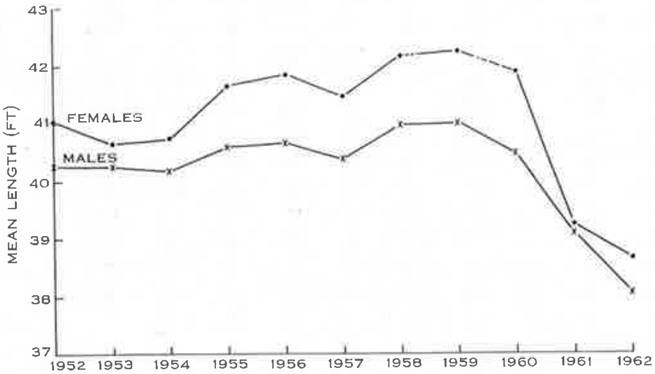

Fig. 22.—Mean lengths of annual catches of male and female humpback whales from the east coast of Australia, 1952–62.

The age composition of catches of females at Norfolk I. was estimated by applying an age–length key obtained from ovarian data collected there from 1956 to 1961, to the length frequency distribution of each year's catch, with the results shown in Table 30.

The age composition of these catches reflect the changes in size composition already discussed. The mean age of the adult males captured from the group IV population, was initially lower, and declined more rapidly, than that of the females (Table 31). The mean age of adults captured from the group V population remained at a relatively high level, falling abruptly in the last 2 years, the mean age of the females falling to a lower level than that of the males.

(*d*) *Physiological Condition*

(i) *Immature Fraction*

Because of the application of the minimum legal length, the immature individuals will always be a smaller proportion of the commercial catch than they are of the whole population. Since the mean length at puberty of females is greater than that of males, i.e. 38 ft 6 in. for females (Chittleborough 1955*b*), and 36 ft 9 in. for males (Chittleborough 1955*a*), commercial catches will contain higher percentages of immature females than of immature males. Nevertheless, the proportions of immature males and females in the catches at a particular locality should remain constant from year to year if the level of selection and the composition of the population do not change. Tables 32 and 33 show that the percentages of immature males and females in samples of the catches from the west and east coasts of Australia have not remained constant during the last decade. Percentages of immature whales generally increased from 1951 to 1954, decreased for a time when the level of selection was raised from 1955, then increased as the mature stock decreased in size. The recent increase in the percentage of immature whales captured from the group V population (Table 33) was far more abrupt than the change in catches from the group IV population (Table 32).

TABLE 25

GROUP IV POPULATION OF HUMPBACK WHALES

Estimated distribution of age in annual catches of males from the west coast of Australia, 1949–62*

Age (yr)	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
2	0	3	3	7	8	6	2	2	3	7	5	4	7	6
3	4	11	40	54	72	70	28	25	27	29	17	50	76	88
4	12	20	81	81	110	118	55	50	67	70	77	54	82	72
5	20	34	129	101	119	123	87	85	125	115	67	67	56	85
6	19	36	131	96	106	106	90	91	81	106	71	37	39	17
7	13	25	92	60	63	61	60	66	77	45	34	18	24	16
8	9	18	66	42	40	37	40	49	45	25	24	13	7	8
9	9	18	65	40	39	34	39	51	39	43	5	8	6	3
10	6	12	41	26	24	21	25	33	26	5	10	5	5	2
11	6	11	37	22	21	17	22	30	17	15	8	2		4
12	5	9	31	19	17	15	18	25	4	12	3	3		
13	5	9	33	21	18	15	20	28	15	17	1		2	
14	3	5	17	10	9	8	11	15	13	4		3		
15	2	4	14	9	8	6	8	12	6					
16	3	5	19	11	11	9	11	17	4	6			1	
17	3	4	17	10	9	7	10	14	3			2	1	
18	2	3	11	7	5	4	6	9						2
19	2	3	10	6	6	4	6	9	4					
20	1	2	8	5	5	4	4	6	6		3			1
20+	11	18	62	39	36	27	38	59	21	10	6	5		
Total catch	135	250	907	666	726	692	580	676	583	509	331	271	306	304

* Using separate ear plug age–length keys of individual samples in each of 1957, 1958, 1959, 1960, 1961, and 1962. For period 1949–56 using combined age–length key; west coast plus east coast, 1956–61.

(ii) *Pregnant Females*

As discussed by Chittleborough (1958*a*), pregnant individuals constitute a greater proportion of the catch of mature females in the Antarctic (summer months) than of the catches of mature females from lower latitudes (winter months). This is because females carrying near-term foetuses are later than other females in their northward migration (Section II(*d*)(ii)), and give birth very soon after reaching temperate regions. On the other hand, as most conceptions take place during August, catches in September and October (also from temperate and subtropical regions) will include females in the very early stages of pregnancy. These small embryos are not easy to locate, and so are not always recorded.

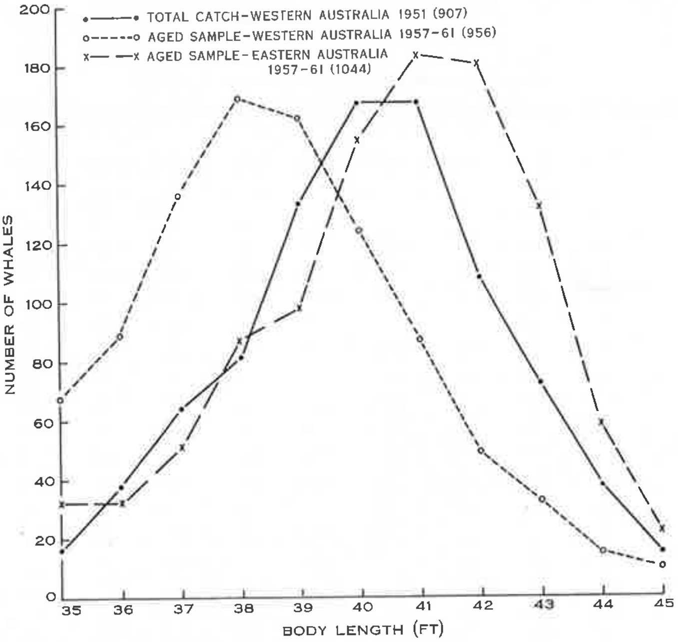

Fig. 23.—Size composition of males in the catch from the west coast of Australia in 1951 compared with size composition of east and west coast samples of males aged by means of ear plugs.

As shown in Section III(*a*)(iv), the average annual birth rate for this species is 0·37, there being 37·2% of the mature females pregnant at one time. No evidence has been found of any variation in the birth rate which might be related to changes in population size brought about by commercial exploitation.

VI. Population Density

(*a*) *Fishing Effort and Catch per Unit Effort*

The abundance of whales at one time or place relative to another can be compared using measurements of catch per unit effort, provided that effort is expressed in terms of a unit which has the same value at all times and places. The unit of effort might be defined as the operation of a vessel, gunner, and crew of standard efficiency or "catching power" in unit area of ocean for unit time. Units of time or area are simple enough, but the catching power is a complex thing, combining the abilities of the vessel, crew, and gunner, to locate, chase, and kill whales. The catching powers of whaling vessels are variable and have been increased over the years as vessels have increased in size, range, speed, and power; as navigational and whale finding aids have been installed; and as gunners and crews have gained in experience.

While all would agree that the unit of effort should be based upon a vessel (and crew) of standard catching power, as yet no one has succeeded in calibrating all the factors affecting the catching power of vessels, so enabling the catching powers of whaling vessels to be measured in terms of a standard unit.

TABLE 26

GROUP V POPULATION OF HUMPBACK WHALES

Estimated distribution of age in annual catches of males from the east coast of Australia, 1952–62*

Age (yr)	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
2	2	1	1		2	2	0	0	0	5	5
3	16	18	23	19	15	14	12	3	26	67	28
4	28	31	31	25	23	28	20	18	13	72	10
5	45	51	53	41	40	43	38	52	41	44	21
6	56	63	65	55	55	57	52	58	69	46	10
7	42	48	47	42	42	27	42	43	41	47	1
8	35	39	38	36	37	32	39	37	44	28	5
9	34	38	36	36	36	22	40	35	45	32	5
10	24	27	27	29	28	27	30	39	30	7	3
11	21	25	24	25	25	30	27	43	17	6	2
12	21	25	24	25	24	17	27	24	24	21	3
13	20	24	23	26	25	30	27	30	30	10	0
14	10	11	12	13	13	16	14	6	16	6	0
15	11	12	12	12	12	17	14	23	10	6	2
16	12	14	14	16	15	17	18	23	16	5	1
17	11	13	13	15	15	9	17	21	13	8	1
18	8	10	9	11	10	13	14	10	4	8	1
19	7	8	8	9	9	4	12	16	14	1	0
20	5	6	5	6	5	7	6	7	8	3	0
20+	40	45	46	53	54	80	62	55	35	26	2
Total catch	448	509	511	494	485	492	511	543	496	448	100

* Using separate ear plug age–length keys of individual samples in each of 1957, 1959, 1960, 1961, and 1962. For 1958, and period 1952–56, using the combined age–length key of all east coast male samples 1957–61.

The unit of effort used so far in whale research is the "catcher's day's work", introduced by Hjort, Lie, and Ruud (1933). This unit refers only to days when hunting was in progress: days lost by individual catchers due to adverse weather, mechanical failure, etc., should not be included as fishing effort. Hjort, Lie, and Ruud were well aware that the catcher's day's work was not a constant unit of effort, but at that time they considered that the variable factors were of minor importance in relation to changes in the size of the stock.

The importance of some of these variable factors can be demonstrated from data obtained in recent years from whaling operations along Australian coasts.

The catcher's day's work is based on a 24-hr period, a variable portion of which is spent in actual whale hunting. In their earlier years of operations, Australian whaling stations generally had greater daily catching power (of the vessels) than the daily processing capacity (of the factory). Because of this, catching vessels were very often allotted a limited number of humpback whales to be killed in a day. In successive years the average catch per catcher's day's work increased (Fig. 24) as the improved factory capacity and efficiency enabled whales to be processed (and hence killed) more rapidly. If the unit of effort (the catcher day) had been constant, such an increase in the rate of catching might well have been interpreted as the result of an increase in availability of whales.

TABLE 27

GROUP V POPULATION OF HUMPBACK WHALES

Estimated distribution of age within catches from Norfolk I. — Males*

Age (yr)	1956	1957	1958	1959	1960	1961	1962
2			1	1			
3	4	3	1	7	4	7	
4	5	4	2	8	7	7	
5	4	3	2	7	7	6	
6	3	4	3	5	5	5	
7	1	1	1	1	1	2	
8	4	5	3	4	6	6	
9	4	4	3	3	4	5	
10	7	8	5	8	9	11	
11	7	8	5	4	5	8	
12	5	5	4	7	7	8	
13	5	6	4	4	6	8	
14	5	6	4	5	6	8	
15	6	5	4	4	5	6	
16	5	4	3	4	3	5	
17	1	2	1	1	1	2	
18	2	3	2	2	2	4	
19	2	2	1	2	3	2	
20	1	1	1	1	1	2	
20+	21	19	13	12	14	22	
Total catch	92	93	63	90	96	124	3

* Applying age–length key from Norfolk I. ear plugs, 1957–61, to length frequency distribution of catches.

On the other hand, the use of the catcher day as a unit of effort can mask a decrease in the availability of whales. For example, Table 34 shows that at Tangalooma in 1960 the catch per catcher's day's work was only slightly less than in previous years, but considerably more hours were spent hunting each day in 1960 than in previous years. In other words, a greater effort had to be expended each day in 1960 in order to maintain a daily rate of catching similar to that in previous years.

The number of hours spent in whaling during each catcher day may vary from one station to another (during the same year). For example, throughout the 1959 season the catcher at Byron Bay maintained an average of 8·8 hr of steaming per day, while in the same year, catchers at Carnarvon averaged 12·7 hr of steaming per day. Catchers operating on these populations of humpback whales in Antarctic areas IV and V were presumably steaming (and hunting) for almost the whole of each 24 hr because of the prolonged period of daylight.

TABLE 28

GROUP IV POPULATION OF HUMPBACK WHALES

Estimated distribution of age in annual catches of females from the west coast of Australia, 1949–62*

Age (yr)	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
2	0	0	1	2	3	3	2	2	2	2	2	2	2	2
3	4	11	27	40	58	66	41	26	40	36	45	36	49	41
4	4	12	29	43	63	72	45	29	44	39	49	39	53	45
5	4	12	28	43	61	70	44	28	43	39	48	38	52	44
6	4	13	33	44	54	60	57	42	58	52	50	35	33	31
7	4	12	29	44	47	52	67	54	67	62	37	25	21	22
8	4	9	22	34	37	38	45	37	46	40	26	19	14	14
9	5	11	26	43	41	41	34	29	36	31	20	15	11	13
10	3	7	15	26	23	25	27	24	28	24	13	8	6	5
11	4	8	18	32	30	30	24	21	24	19	13	9	6	4
12	3	7	15	27	24	24	17	15	18	14	14	10	6	3
13	3	6	11	22	20	21	16	16	16	12	8	6	4	2
14	2	4	9	16	14	15	16	15	16	13	5	4	2	1
15	1	3	6	12	11	11	16	16	16	12	4	3	2	0
16	2	6	11	23	21	24	21	20	21	16	9	6	3	2
17	0	1	2	4	4	5	13	12	12	10	4	2	1	3
18	1	2	3	6	5	6	13	13	10	8	4	2	2	1
19	1	0	1	2	2	2	6	6	6	5	1	1	0	1
20	1	1	2	5	5	5	7	6	6	4	2	1	0	1
20+	5	12	22	48	48	47	32	33	27	20	15	13	5	4
Total catch	55	137	310	516	571	617	543	444	536	458	369	274	272	239

* Using separate ovary age–length keys, 1949–54, 1955–58, 1959–61, on length frequency of catches. Ovary group "O" converted to age on ear plug data.

The number of hours per day spent in whaling can vary, during a season at one locality, inversely to changes in density of whales passing that point. For example, at Tangalooma in 1960, from June 6 to 15 there was a mean of 10·35 hunting hours per catcher day. From July 6 to 15 (height of migration past this station) a mean of 7·95 hunting hours per catcher day, and from August 6 to 15 (end of northward migration) a mean of 10·68 hunting hours per catcher day.

The hours spent hunting on a particular day might be reduced because of adverse weather, yet the unit of effort, the catcher's day's work, rates such a day as of equivalent fishing effort as a day when it was possible to stay on the whaling grounds throughout daylight hours. This effect of weather upon the hours spent whaling might be expected to occur at random, so that it might not be important when comparing rates of catching over long periods of time. Nevertheless, whalers have claimed that adverse weather conditions have been the real cause of an apparent decrease in density of whales from one year to another (Chittleborough 1960*a*).

TABLE 29

GROUP V POPULATION OF HUMPBACK WHALES

Estimated distribution of age in annual catches of females from the east coast of Australia, 1952–62*

Age (yr)	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
2	0	1	1	1	1	1	1	1	1	2	5
3	13	18	21	17	15	18	12	15	20	45	18
4	14	20	22	19	17	20	13	17	22	50	12
5	14	19	22	18	16	20	13	17	21	49	11
6	15	20	23	22	20	21	18	22	30	27	10
7	12	16	16	17	16	16	15	17	24	17	4
8	13	17	17	18	19	19	17	21	27	17	2
9	10	12	11	14	16	14	13	17	20	11	1
10	8	10	10	12	15	12	12	16	17	8	2
11	8	10	9	12	14	12	13	16	18	9	2
12	7	8	8	11	13	11	11	15	16	7	2
13	5	6	6	8	10	8	9	11	12	6	1
14	5	6	5	7	9	7	7	10	10	4	0
15	3	3	4	5	6	5	6	7	8	4	0
16	6	7	7	10	12	10	11	14	15	7	0
17	2	2	4	5	5	5	5	7	7	3	0
18	2	2	2	3	4	3	4	5	5	2	0
19	1	1	2	2	2	2	2	4	3	1	1
20	1	1	2	2	2	3	3	3	4	1	0
20+	11	12	15	23	23	22	24	32	34	13	2
Total catch	150	191	207	226	235	229	209	267	314	283	73

* Applying age–length key for combined ovary samples east coast 1952–61, to length frequency distribution of each year's catch. Ovulation group "O" distributed on ear plug data.

The examples given above show that the catcher day is not a constant unit of time. In an attempt to obtain a more precise unit within which to measure fishing effort, all available ships' logs from Australian whaling companies were examined. Where a log had been kept in detail, it was generally possible to dissect each day's operations into various categories, namely:

(1) Total steaming time; all the time absent from moorings, irrespective of duties.

(2) Steaming time on that day's whaling; this excludes time spent away from moorings when engaged in bunkering, victualling, moving whales moored from the previous day's catch, and other transport duties.

(3) Steaming time hunting (and killing) whales; this excludes time spent steaming out to whaling grounds from the previous night's anchorage, and also

excludes time spent towing whales back to the station (and returning to the whaling grounds). Obviously the hunting time is restricted to daylight hours, whereas (2) may include several hours of darkness.

The "catcher's steaming hour", from category (2), is a more precise measure of whaling effort than the catcher's day's work, as any time at anchor when the factory does not require more whales, is omitted. It also eliminates parts of days lost due to minor repairs, refuelling, adverse weather, etc. Hours spent towing the catch back to the station are included in this unit of effort. Certain vessels can tow fewer whales, and at slower speeds, than others, so that their average catch per steaming hour may be depressed below that of other vessels of equal hunting efficiency but more suited to towing whales.

TABLE 30

GROUP V POPULATION OF HUMPBACK WHALES

Estimated distribution of age within catches from Norfolk I. — Females*

Age (yr)	1956	1957	1958	1959	1960	1961	1962
3	6	2	2	2	6	5	
4	6	2	2	3	6	6	
5	6	2	2	3	6	6	
6	4	3	3	3	5	4	
7	3	1	3	2	6	2	
8	2	1	2	2	4	1	
9	3	2	4	3	4	2	
10	1		2	2	2	1	
11	2	2	3	3	5	2	
12	1	1	2	3	3	1	
13	1		2	2	1	1	
14	1	1	2	1	1	1	
15	2	1	2	3	2	1	
16	2	1	3	3	3	1	
17	1	1	2	2	1	1	
18	1		1	1	1		
19							
20	1		2	3	2	1	
20+	15	7	18	19	16	10	
Total	58	27	57	60	74	46	1

* Applying age–length key from ovaries Norfolk I., 1956–61, to length frequency distribution of catches.

The "catcher's hunting hour", derived from category (3) above, is in theory the most precise measure of whaling effort. However, many ships' logs had not been entered in sufficient detail for this to be extracted for each day's operations, and consequently the catcher's steaming hours had to be taken as measure of effort for vessels operating at Point Cloates, Carnarvon, and Albany.

At Tangalooma and Byron Bay, catchers' hunting hours could be tallied. A catcher's steaming hour at the former station was not equal to a catcher's steaming hour at other stations, because at Tangalooma one of the whaling vessels was stationed on the whaling grounds each day to act solely as a towing vessel. Thus, although the catching vessels might tow some whales to the station, their steaming time included a much lower proportion of towing time than did the steaming time of catchers at other stations.

The effective length of the catcher day has also been increased by mooring the catchers closer to the whaling grounds, and by the use of spotting aircraft. The increased effort achieved by these means has been calculated in terms of catcher hours (Chittleborough 1962).

TABLE 31

MEAN AGES OF ADULT HUMPBACK WHALES (OVER 5 YEARS OLD) IN CATCHES FROM THE WEST AND EAST COASTS OF AUSTRALIA

Year	Males		Females		Year	Males		Females	
	Number Taken	Mean Age (yr)	Number Taken	Mean Age (yr)		Number Taken	Mean Age (yr)	Number Taken	Mean Age (yr)
		West coast					*East coast*		
1949	99	11·16	43	11·98	1949	—		—	
1950	182	10·82	102	11·52	1950	—		—	
1951	654	10·78	225	11·04	1951	—		—	
1952	423	10·58	388	11·72	1952	357	11·48	109	11·34
1953	417	10·29	386	11·47	1953	408	11·52	133	10·99
1954	375	9·86	406	11·37	1954	403	11·52	141	11·33
1955	408	10·59	411	11·20	1955	409	12·01	171	11·94
1956	514	11·24	359	11·65	1956	405	11·99	186	12·06
1957	361	9·56	407	10·96	1957	405	12·87	170	11·98
1958	288	8·61	342	10·66	1958	441	12·32	170	12·36
1959	165	8·02	225	10·13	1959	470	12·20	217	12·52
1960	96	8·47	159	10·24	1960	416	11·31	250	12·08
1961	85	7·31	116	9·22	1961	260	10·75	137	10·83
1962	53	8·02	107	9·00	1962	36	10·08	27	9·12

In the conversion of aircraft flying hours into equivalent catcher hour units, a rather arbitrary relation was assumed, i.e. 1 aircraft flying hour equals 5 catcher steaming hours. This relation can be calculated where sighting records were made simultaneously from catchers and aircraft operating in the same area at the same time. For example, off Albany in the winter of 1961, two catchers sighted 226 humpback whales in a total of 605 steaming hours. Then 2·68 hours of steaming were required to sight one humpback whale. In the same period, the spotting aircraft sighted 241 humpback whales in 144·6 flying hours, i.e. 0·60 flying hours for each humpback whale sighted. In this instance, 2·68 catcher steaming hours were equivalent to 0·60 aircraft flying hours, or 4·7 catcher steaming hours were equivalent to 1 flying hour.

The relation between the catcher's steaming hour and the aircraft's flying hour would no doubt vary for different aircraft, catchers, personnel, and localities, but in the case where the ratio could be calculated, the result was close to the value of 5 catcher steaming hours is equivalent to 1 aircraft flying hour, which has been used in calibrating fishing effort.

TABLE 32

GROUP IV POPULATION OF HUMPBACK WHALES

Immature whales in samples of catches from the west coast of Australia

Year	Males				Females			
	Total Catch	Number Examined	Number Immature*	Percentage Immature*	Total Catch	Number Examined	Number Immature and Pubertal	Percentage Immature and Pubertal
1951	907	395	36	9·1	310	90	20	22·2
1952	666	161	35	21·7	516	278	59	21·2
1953	726	111	37	33·3	569	246	93	37·8
1954	692	—	—	—	617	150	44	29·3
1955	580	—	—	—	538	—	—	—
1956	676	—	—	—	443	279	34	12·2
1957	583	488	66	13·5	536	521	134	25·7
1958	509	439	79	18·0	458	438	114	26·0
1959	331	254	88	34·6	369	352	124	35·2
1960	271	208	54	26·0	274	263	120	45·6
1961	306	291	137	47·1	272	263	157	59·7
1962	304	280	142	50·7	239	230	129	56·1

* Testes weights at or less than 4 kg.

TABLE 33

GROUP V POPULATION ON HUMPBACK WHALES

Immature whales in samples of catches from the east coast of Australia

Year	Males				Females			
	Total Catch	Number Examined	Number Immature*	Percentage Immature*	Total Catch	Number Examined	Number Immature	Percentage Immature
1952	448	233	32	13·7	150	102	24	23·5
1953	509	200	25	12·5	191	120	37	30·8
1954	511	298	36	12·1	207	148	49	33·1
1955	494	—	—	—	226	114	24	21·1
1956	485	60	2	3·3	235	139	25	18·0
1957	492	215	13	6·1	229	183	49	26·8
1958	511	205	17	8·3	209	121	29	24·0
1959	543	273	8	2·9	267	205	46	22·4
1960	496	293	22	7·5	314	212	44	20·8
1961	448	446	151	33·9	283	263	143	54·4
1962	100	100	44	44·0	73	73	39	53·4

* Testes weights at or less than 4 kg.

When using the catch per unit effort to compare the abundance of whales from one year to another, it is important that the effort was applied during the same period of time in those years, because as shown by Chittleborough (1962, Figs. 4, 5, and 12; 1963 Fig. 6; and Figs. 3 and 4 in the present paper), the abundance of whales changes during the season, as the northward and southward migrating streams pass each shore station. The opening date and length of season has fluctuated at each Australian whaling station, but in most cases the stations were operated throughout the greater part of the northward migration. At Carnarvon the relative abundance (catch per unit effort) of humpback whales was measured each year from June 25 to August 26 (this being the only catching period common to every year from 1951 to 1962). At Tangalooma the relative abundance of humpback whales was measured each year from June 10 to August 5.

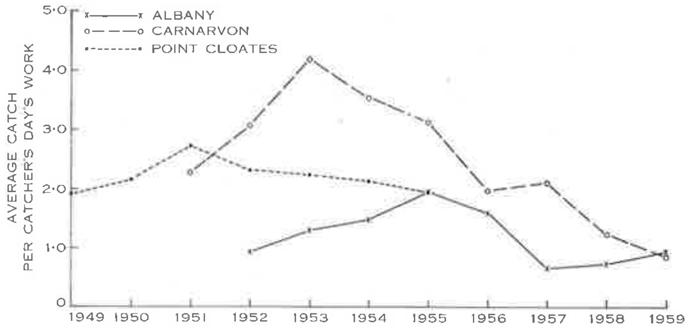

Fig. 24.—Average annual catch (humpback whales) per catcher's day's work at shore stations on the west coast of Australia.

In the measurement of fishing effort, variations in the "catching power" of whaling vessels present more difficulties than the units of time. The Australian whaling industry has employed as wide a range of types of vessels for hunting whales (Table 35), as could be found engaged in whaling in most other countries. Vessels differed very greatly in size, age, speed, manoeuvrability, towing power, and ability to operate successfully in heavy seas. Two small speedy launches, working together as one unit in coastal whaling, and the large steel "Antarctic"-type chaser, were not equivalent units of effort, nor would the relative efficiency of one type to the other, have remained the same under varied operating conditions (such as weather, or configuration of the coastline).

Table 34 shows that similar vessels, operated in the same locality, at the same time, by gunners of similar experience, achieved similar rates of catching. When dissimilar vessels, operating in one locality at the same time, are compared (Fig. 25), their contrasting rates of catching reflect their various efficiencies, during a period when whales were plentiful. However, when the population had been depleted, rates of catching converged to similar low levels, indicating that differences in catching power were of little importance when whales were scarce.

A number of the catchers have operated in each of the past 12 seasons on the Australian coast. This simplifies the analysis of fishing effort, because as pointed out by Hjort, Lie, and Ruud (1933), operations by the same vessels can be compared directly from one season to another. For present purposes, four catchers which

TABLE 34

OPERATIONS OF CATCHERS AT TANGALOOMA DURING PERIOD JUNE 10–AUGUST 5 OF EACH SEASON, 1953–62

Year	Vessel	Total Days Hunting	Total Hours Hunting	Total Humpback Whales Killed	Average Hunting Hours per Day	Average Whales per Catcher's Day's Work	Average Whales per Hunting Hour	Average Hours per Whale
1953	*Kos* I	55	247	171	4·49	3·11	0·69	1·44
1954	*Kos* VII	50	291½	157	5·83	3·14	0·54	1·86
1955	*Kos* II	45	312½	234	6·94	5·20	0·75	1·34
	Kos VII	56	326	263	5·82	4·70	0·81	1·24
	Total	101	638½	497	6·32	4·92	0·78	1·28
1956	*Kos* II	55	367	265	6·67	4·82	0·72	1·38
	Kos VII	55	374	257	6·80	4·67	0·69	1·46
	Total	110	741	522	6·74	4·75	0·70	1·42
1957	*Kos* I	55	387½	270	7·05	4·91	0·70	1·44
	Kos II	55	373½	274	6·79	4·98	0·73	1·36
	Total	110	761	544	6·92	4·95	0·71	1·40
1958	*Kos* I	55	389½	291	7·08	5·29	0·75	1·34
	Kos II	54	398½	300	7·38	5·56	0·75	1·33
	Total	109	788	591	7·23	5·42	0·75	1·33
1959	*Kos* I	57	401½	302	7·04	5·30	0·75	1·33
	Kos II	57	418	305	7·33	5·35	0·73	1·37
	Total	114	819½	607	7·19	5·32	0·74	1·35
1960	*Kos* I	57	532½	270	9·34	4·74	0·51	1·97
	Kos II	57	528½	284	9·27	4·98	0·54	1·86
	Total	114	1061	554	9·31	4·86	0·52	1·92
1961	*Kos* I	56	534¾	119	9·55	2·13	0·22	4·49
	Kos II	57	550½	131	9·66	2·30	0·24	4·20
	Total	113	1085¼	250	9·60	2·21	0·23	4·34
1962	*Looma* II	47	488¾	38	10·40	0·81	0·08	12·86
	Looma III	47	500	30	10·64	0·64	0·06	16·67
	Total	94	988¾	68	10·52	0·72	0·07	14·54

hunted each year on the west coast, and two which hunted each year on the east coast, have been used as standard units of catching power. The steaming or hunting hours of these catchers working in the same localities each year, and over the same period of time (during the northward migration), have been assessed. Adjustments have been made to the effort in those years where the effective hours were increased by the introduction of spotting aircraft or a change of moorings. These adjustments have been made in terms of equivalent steaming or hunting hours by the catchers used as the standard.

TABLE 35

SOME WHALE CATCHING VESSELS USED BY AUSTRALIAN COMPANIES

Vessel	Hull	Length (ft)	Tonnage		Engine
			Gross	Net	
Carnarvon	Steel	160	598	216	Steam
*Tangalooma**	Steel	147	392	294	Steam
Robert Moore	Steel	138	374	155	Steam
Gascoyne	Steel	137	344	123	Steam
Kos I	Steel	125	254	97	Steam
Kos II	Steel	125	254	97	Steam
Kos VII	Steel	125	253	108	Steam
Minilya	Steel	116	248	118	Steam
Cheynes	Steel	112	248	approx. 80	Steam
Haeremai Star	Wood	112	120	78	Twin diesel
Point Cloates	Wood	112	118	80	Twin diesel
Vigilant	Steel	98	101	26	Twin diesel
Norfolk Whaler	Wood	119	217	91	Twin diesel
Byrond I	Wood	109	113	90	Twin diesel
Cascade	Wood	36	Approx. 5 tons (dead weight)		Petrol
Kingston	Wood	36	Approx. 5 tons (dead weight)		Petrol

* Used for towing only.

The unit of effort used for the Australian seasons prior to 1955 was not precisely the same as that from 1955 onwards. Owing to a reduction in quota, a more vigorous management policy made the unit fishing time more effective from 1955. Assuming that the mortality coefficient of 1954–55 was the mean of the 1953–54 and the 1955–56 mortalities, then the effort units in 1954 and earlier years have to be reduced by a factor of 0·7 to equate them with the effort units of 1955 and later years.

From the adjusted effort, in standard units, applied each year by the same catchers operating in the same locality over the same period of time, and the catch of humpback whales taken by these same vessels under those conditions, indices of relative abundance (catch per unit effort) have been calculated for each year (Table 36).

Estimates of the total annual effort on the west coast of Australia were obtained for each winter season by multiplying the adjusted effort of the standard west coast catchers by the ratio of the total west coast catch to the catch by the standard catchers. The Antarctic (area IV) effort was estimated by dividing the catch in each summer by the mean catch per unit effort of the standard west coast catchers during the two adjacent winters (Table 37). Corresponding estimates of total annual effort applied within the group V population were made using the data from the catchers used as a standard on the east coast of Australia, and the annual catches from the various localities within the group V population (Table 38).

Humpback whale fishing effort in Antarctic areas IV and V had to be estimated in terms of the Australian units, partly because full details of the effort data were not available from these areas, and also because a variety of species was being hunted simultaneously in these southern feeding grounds, making it extremely difficult to separate from the overall Antarctic effort, that portion which had been applied to humpback whales.

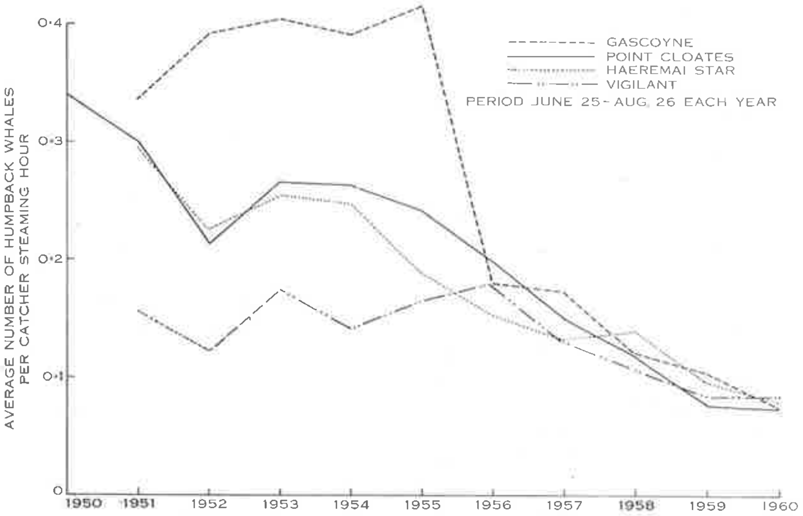

Fig. 25.—Catch per unit effort by four catchers operating on the west coast of Australia during the same period each year.

The total effort expended within a particular population of humpback whales and responsible for the estimated fishing mortality from a particular pair of years (Section VII), was estimated as the mean effort from the temperate regions in the winters of those 2 years, plus the corresponding Antarctic effort in the intervening summer.

(*b*) *Changes in Abundance*

Using the well-documented operations of certain Australian catchers, and after eliminating or adding weighted components for factors which varied the fishing effort in a particular year (where some measure could be made of such factors), the estimated catch per unit effort gives an index of abundance of humpback whales from one season to another (Table 36). The values from the west coast of Australia cannot be compared directly with those from the east coast of Australia as the catching power of the vessels used as standards in the two localities were not the same, and the unit of effort used on the west coast (catcher's steaming hour) was not the same as that used on the west coast (catcher's hunting hour). These differences cannot be resolved entirely, but the approximate relation would be that 1 standard unit of effort for the west coast was equivalent to 0·5 standard units for the east coast. The indices of abundance (catch per unit effort) are plotted in Figure 26 using this relation.

The two populations appear from Figure 26 to have been initially of similar size. Although there was some decline in numbers soon after post-war whaling began, the abundance of humpback whales in the group IV population continued to be relatively high until 1954, whereas the group V population was relatively abundant until 1959. Since those years the populations have declined in numbers, the group V population decreasing more rapidly than the group IV population.

TABLE 36

ADJUSTED EFFORT, HUMPBACK WHALE CATCH, and CATCH PER UNIT EFFORT, BY CATCHERS ADOPTED AS STANDARD FOR OPERATIONS ON GROUP IV AND V POPULATIONS

Year	Standard Catchers* from Group IV Population			Standard Catchers† from Group V Population		
	Adjusted Effort (steaming hours)	Humpback Whale Catch (number)	Catch per Unit Effort	Adjusted Effort (hunting hours)	Humpback Whale Catch (number)	Catch per Unit Effort
1950	341	162	0·475	—	—	—
1951	995	422	0·424	—	—	—
1952	1568	544	0·347	—	—	—
1953	1465	517	0·353	176	171	0·972
1954	1852	650	0·351	208	157	0·755
1955	2378	580	0·244	638	497	0·779
1956	2631	467	0·178	741	522	0·704
1957	3351	489	0·146	761	544	0·714
1958	2847	350	0·123	788	591	0·750
1959	3015	271	0·090	820	607	0·740
1960	3957	245	0·062	1061	554	0·522
1961	6557	358	0·055	1085	250	0·230
1962	5524	284	0·051	989	68	0·069

* The same four catchers operating on the west coast of Australia from June 25 to August 26 each year.

† Two catchers operating on the east coast of Australia from June 10 to August 5 each year.

In 1962 the group V population was apparently smaller than the group IV population. This difference may have been even greater than indicated by the data in Figure 26, because in 1962 the two catchers previously used as the standard for the east coast data were replaced by two more modern catchers of considerably greater catching power. However, no adjustment was made to the data in order to allow for this change in catching power, because it has been shown above (Fig. 25) that when the abundance of whales has been reduced to a low level, differences in catching power of individual catchers are of minor importance.

Jonsgård, Ruud, and Øynes (1957) claimed that in the Antarctic during the period from 1950 to 1956, the group IV and V populations of humpback whales had increased in abundance relative to the stocks of blue and fin whales. This has little meaning, for if blue and fin whale stocks were declining at faster rates than the humpback whale stocks, the humpback whales could appear to be relatively more abundant than the other species, yet decreasing themselves.

TABLE 37

TOTAL EFFORT IN TERMS OF STANDARD CATCHERS EXPENDED ON THE GROUP IV POPULATION OF HUMPBACK WHALES EACH YEAR FROM 1949 TO 1962

Year	Effort on Males			Effort on Females		
	West Coast Australia	Antarctic Area IV	Total* Effort	West Coast Australia	Antarctic Area IV	Total* Effort
1949	278			113		
		745	1147		895	1096
1950	526			288		
		1040	2372		1431	1940
1951	2138			731		
		1415	3444		1505	2615
1952	1920			1487		
		294	2282		257	1809
1953	2057			1618		
		378	2393		355	2043
1954	1972			1758		
		40	2215		54	2046
1955	2378			2226		
		1517	4610		2389	4753
1956	3808			2501		
		0	3901		0	3087
1957	3994			3673		
		0	4067		0	3700
1958	4140			3727		
		6028	9939		7178	11,094
1959	3682			4106		
		368	4398		500	4765
1960	4376			4424		
		51	5041		17	4720
1961	5604			4982		
		453	6212		604	5421
1962	5913			4651		

* Catcher steaming hours.

(c) *Changes in Distribution*

As humpback whales have decreased in numbers from year to year, the catches at each Australian shore station have been dispersed over wider areas. This has not been caused by a change in the behaviour of the migrating humpback whales, but because of the lowered density of the whales, forcing the catchers to scour larger areas of ocean in order to locate humpback whales of legal size.

A typical example of the increased dispersion of catches is given in Figures 27 and 28, showing the distribution of the catches by the Carnarvon station in 1951 and 1962, respectively. By 1962 the catch was dispersed farther offshore as well as for a greater distance along the coast than in 1951, increasing accessibility and vulnerability, respectively.

In the 1951 season, the whales were captured within 40 miles of the coast, almost all within Shark Bay. Other whales which passed this latitude outside of Shark Bay were not exposed to hunting at that time, i.e. they were not accessible to the whaling operations of that year. By 1962 the catchers (assisted by spotting aircraft) had extended their operations up to 70 miles west of the whaling station, stretching right across the coastal migration path. The whole of this population was then exposed to hunting.

TABLE 38

TOTAL EFFORT IN TERMS OF STANDARD CATCHERS EXPENDED ON THE GROUP V POPULATION OF HUMPBACK WHALES EACH YEAR FROM 1952 TO 1962

Year	Effort on Males					Effort on Females				
	East Coast Australia	Norfolk I.	New Zealand	Antarctic Area V	Total* Effort	East Coast Australia	Norfolk I.	New Zealand	Antarctic Area V	Total* Effort
1952	461		75			154		49		
				218	782				300	523
1953	524		67			197		45		
				0	702				0	309
1954	677		136			274		102		
				596	1365				834	1196
1955	634		91			290		53		
				123	953				139	564
1956	689	131	114			334	82	90		
				0	948				0	489
1957	689	130	143			321	38	113		
				0	938				0	461
1958	681	84	149			279	76	95		
				615	1628				573	1112
1959	734	122	245			361	81	185		
				645	1980				830	1645
1960	950	184	435			602	142	258		
				359	2496				420	1701
1961	1948	539	217			1230	200	130		
				0	2265				0	1381
1962	1449	43	333			1058	14	129		

*Catcher hunting hours.

In 1951, the extreme range of the catch from north to south was less than 60 miles (Fig. 27). A whale swimming at 2½ knots would then take less than 24 hr to pass through the whaling area. Since half of the distance would have been travelled during darkness, some individuals could have passed through the whaling grounds without having been sighted. Thus vulnerability would have been relatively low within the whaling area occupied in 1951.

In 1962, the extreme range of the catch from north to south extended over 160 miles. A whale travelling at 2½ knots would in that year, take some 64 hr to migrate through the whaling area, so being exposed to hunting on 3 successive days. Vulnerability would then be very high during favourable weather.

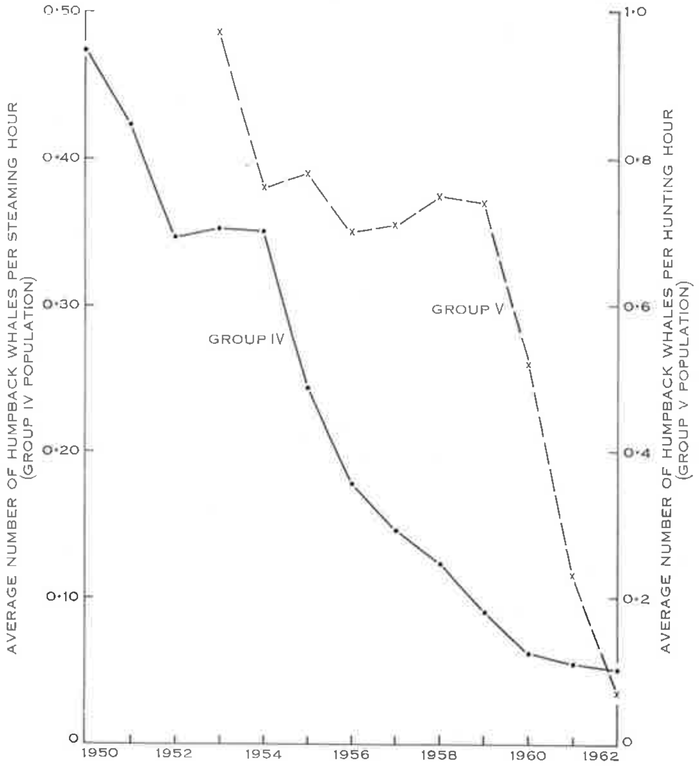

Fig. 26.—Relative abundance (catch per unit effort) of humpback whales in group IV and V populations as measured each winter on the west and east coasts of Australia.

Similar changes in the distribution of the catches have been recorded for the whaling stations at Albany, Tangalooma, Byron Bay, and Norfolk I. (Chittleborough 1962).

VII. MORTALITY

(a) *Instantaneous Total Mortality Coefficients*

Estimates of total mortality have been made from the age composition of Australian catches (Tables 25–30), weighted according to the total effort (Tables 37 and 38) expended in making these catches. The catch in each season from each age group was divided by the value for total effort expended in the corresponding season, so that each of the Tables 25–30 was converted to age composition per unit of effort. This gives an index of abundance of whales in each age group at that time and locality, with the exception of some of the juvenile age groups which were not fully recruited into the catchable stock.

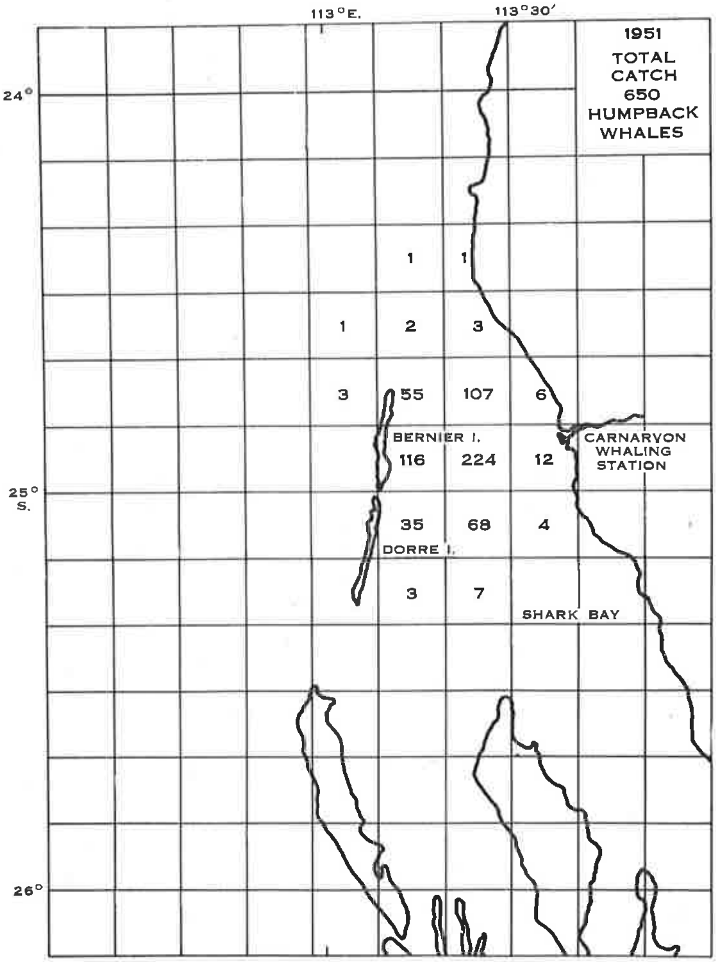

Fig. 27.—Area off Carnarvon whaling station marked in squares, 10 × 10 nautical miles, showing in each square the number of humpback whales killed in 1951.

Let U_i be the catch per unit of effort at age i in a specified season and locality, and U_{i+1} the catch per unit effort at age $i+1$ in the same locality but one year later. Then:

$$U_{i+1}/U_i = S = e^{-Z},$$

where Z is the total mortality coefficient. The survival rate (S) was calculated for each fully recruited age group in pairs of successive years, separate calculations being made for males and females on both the west and east coasts of Australia. For the older age groups (those exceeding 15 years of age) the numbers recorded in the catches were so few that the individual estimates of *S* were unreliable. For these age groups a mean survival rate was calculated by the ratio of the total catch per unit of effort for all age groups from 15 years and over in year $i+1$, to the total catch per unit effort for all age groups from 14 years and over in year *i*.

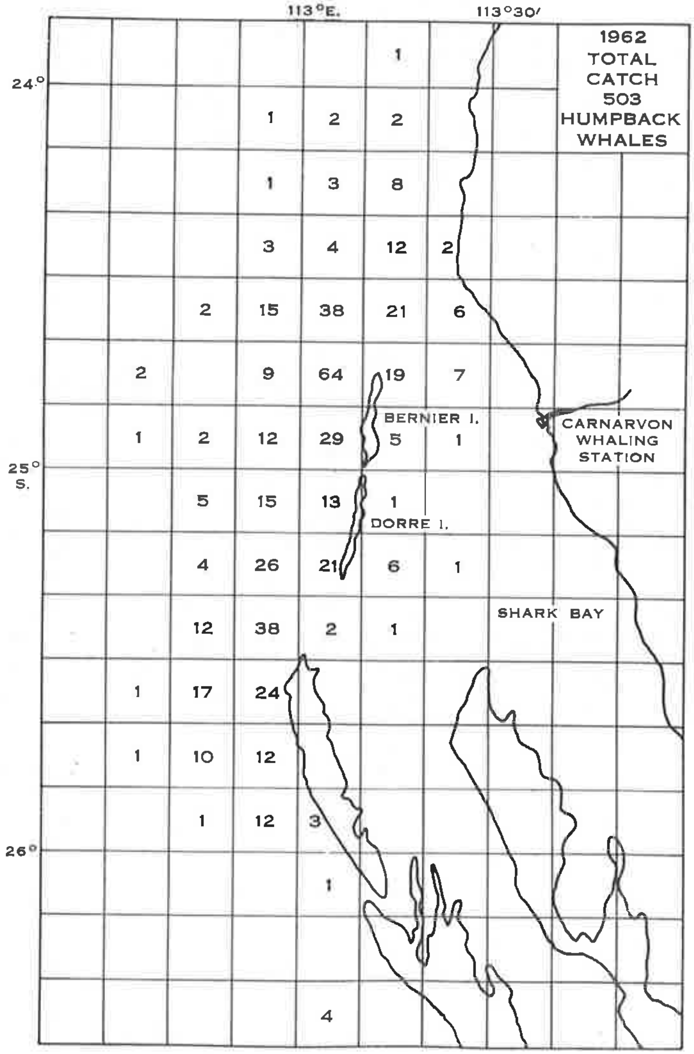

Fig. 28.—Area off Carnarvon whaling station marked in squares 10 × 10 nautical miles, showing in each square the number of humpback whales killed in 1962.

The instantaneous mortality coefficient (*Z*) was obtained for each age group from the value of *S* using the tables prepared by Ricker (1958). This gives a number of estimates of *Z* for each sex, locality, and pair of years. A mean value of *Z* for each sex, locality, and pair of years was obtained, weighting the individual estimates of Z for each age group by the number of whales upon which the estimate was based. Total mortality from 1954 to 1955 was not calculated, owing to the change in the application of effort between these years, as described in Section VI (*a*).

TABLE 39

INSTANTANEOUS MORTALITY COEFFICIENTS (Z) CALCULATED FROM CATCH AT AGE AND EFFORT DATA ON WEST AND EAST COASTS OF AUSTRALIA

Year	1949–50	1950–51	1951–52	1952–53	1953–54	1955–56	1956–57	1957–58	1958–59	1959–60	1960–61	1961–62
Group IV population												
Males	0·232	0·369	0·600	0·390	0·382	0·425	0·803	0·657	1·091	0·876	0·847	0·900
Females	0·226	0·318	0·315	0·283	0·215	0·360	0·391	0·366	0·803	0·670	0·802	0·539
Group V population												
Males	—	—	—	0·254	0·441	0·264	0·198	−0·010	0·194	0·476	1·562	1·577
Females	—	—	—	0·325	0·507	0·167	0·233	−0·014	0·139	0·512	1·561	1·753

The mortality coefficients derived from these calculations (Table 39) apply to the adult portion of the relevant stock, since the juvenile age groups in most cases had not been fully recruited.

Table 39 shows that in the group IV population, total mortality was initially about the same in the two sexes, but as whaling progressed, total mortality of males increased to much higher levels than that of females. This is consistent with the earlier changes in the composition of catches of the more heavily fished males (see Section V).

TABLE 40

PROVISIONAL ESTIMATES OF TOTAL MORTALITY COEFFICIENTS FROM NEW ZEALAND CATCHES

Year	1955–56	1956–57	1957–58	1958–59	1959–60	1960–61	1961–62
Males	0·79	0·14	1·02	0·22	0·81	1·60	1·77
Females	0·36	0·16	0·31	0·14	0·09	1·62	2·15
Mean	0·58	0·15	0·67	0·18	0·45	1·61	1·96

On the east coast of Australia (group V population) total mortality rose moderately in 1959–60, then became very high in 1960–61 and 1961–62 (Table 39), even though the catches in these years had not been unusually high (Table 2).

An independent estimate of mortality in 1961–62 can be made from the frequency of sightings of humpback whales off the east coast of Australia during the two winter seasons. At Tangalooma 88·2 humpback whales were sighted per 100 catcher hunting hours in 1961, and 38·6 per 100 catcher hunting hours in 1962, both values being for the same period (June 12–August 6). These values give a survival rate (*S*) of 0·44, which is equivalent to a total mortality coefficient (*Z*) of 0·83. The mortality calculated from the sighting records is lower than the corresponding estimates of mortality from the catch data, but this is to be expected, since the former refers to the whole population (most of the members of which were, in those years of observation, below the minimum legal length), while the latter refer only to the adult (highly exploited) part of it.

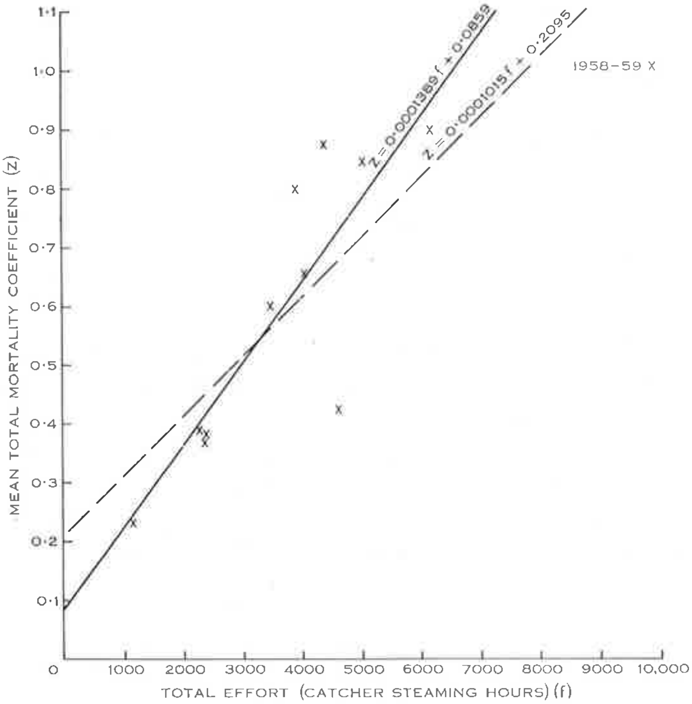

Fig. 29.—Mortality and effort, group IV male humpback whales; broken line regression on all points, solid line regression excluding 1958–59 value.

Further estimates of *Z* for the group V population can be derived from the catches in Cook Strait, N.Z., making certain assumptions, mainly with regard to effort. Assuming that the growth rate of humpback whales in New Zealand was the same as for Australian specimens, estimates were made of the age composition of New Zealand catches from 1955 to 1962, by applying to the length frequency distribution of males and females killed in New Zealand (records from International Whaling Statistics), the age–length keys derived from the Australian material.

There were no records of measurement of effort expended in taking the New Zealand catches which were made throughout the whole of the northward migration each year, searching being conducted from an elevated position on the shore. The increase in the annual catch from 1955 to 1960 (Table 2) was due to better searching and improved plant efficiency rather than to an increase in the stock.

The catch per unit effort of each age group was calculated assuming that the total catch per unit effort had been constant from 1955 to 1960 (i.e. the stock did not increase), and that the effort in 1961 was the same as that in 1960. In 1962, two sighting lookouts were operated and approximately half of the sightings were made from the new lookout, so that the effort expended in 1962 was taken to be double that of 1960.

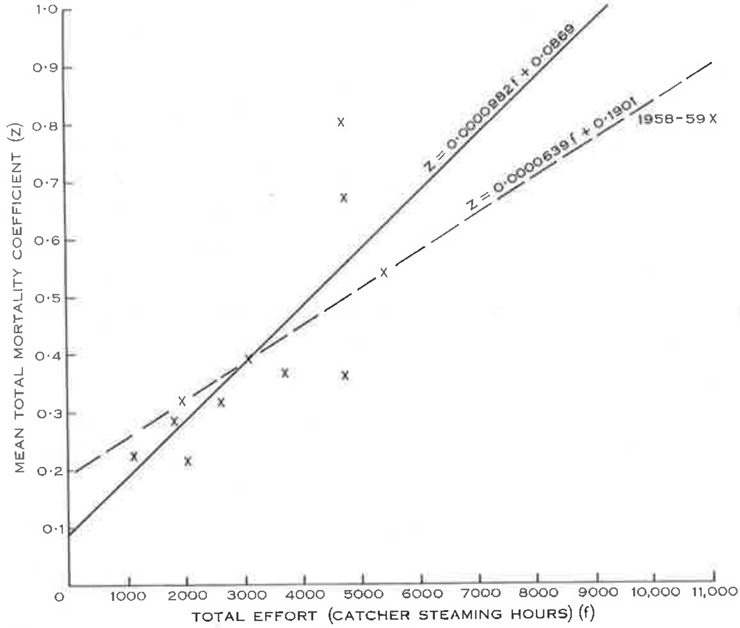

Fig. 30.—Mortality and effort: group IV female humpback whales; broken line regressionon all points, solid line regression excluding 1958–59 value.

Total mortality coefficients were then estimated between pairs of years, using only those age groups which were fully recruited, following the same procedures as for the data from the Australian coasts. The mean values (Table 40) were more variable than the estimates of Z from the data collected on the east coast of Australia but the values derived from the data from both localities rose to similar high levels in 1960–61 and 1961–62.

The results from two widely separated localities (east coast of Australia and New Zealand) show a very sharp rise in total mortality within the group V population from 1960 to 1962. The evidence of at least partial segregation into separate breeding units within this population during the winter (breeding season) suggests that the similar and high mortalities recorded at the same time in different localities were not due entirely to the fishing in those regions, but had a common origin. Recent catches reported from Antarctic area V (included in the total effort recorded in Table 38) have not been sufficiently large to account for these very high mortality coefficients.

There are three possible explanations:

(1) That the group V stock of humpback whales has recently changed its long established migration paths. This hypothesis is contradicted by widely scattered and independent observers throughout the South Pacific islands, on ships, and on the Australian coast, all reporting a great reduction in the number of humpback whales during the winter seasons of 1961 and 1962.

(2) That there was increased natural mortality (of epidemic proportions) due to disease, parasitic infections, or starvation. This also has no supporting evidence, as the few humpback whales captured were in good health, and had a normal thickness of blubber, and gave a normal oil yield.

(3) That substantial catches of humpback whales had recently been taken from this stock in addition to those shown in the available records, in a region where the humpback whales from New Zealand and the east coast of Australia can both be fished simultaneously, i.e. Antarctic area V.

There is some evidence supporting the last hypothesis. Although no humpback whales were reported to have been taken from Antarctic area V in the summer of 1961–62 (Table 2), two marks, previously fired into humpback whales, were recovered from whales killed within Antarctic area V during that summer. The information reported with respect to these marks is shown in the following tabulation:

Mark No.		Release	Recapture
15898	Date	October 12, 1959	December 19, 1961
	Locality	East coast of Australia; 27°S., 153°30′E.	62°21′S., 166°10′E.
	Species	Humpback whale	Sperm whale
	Size	Calf, 2–3 months old with cow	43 ft 8 in. (13·3 m), male
21815	Date	June 2, 1961	February 24, 1962
	Locality	Cook Strait, N.Z.	66°50′S., 162°59′E.
	Species	Humpback whale	Fin whale
	Size	—	65 ft 4 in. (19·9 m), female

There is no likelihood that there could have been any confusion as to the species at the time that these marks were fired into the whales. Some error must have been made with regard to the whales from which the marks were recovered, but whatever the explanation of the obviously erroneous recovery data, the evidence is clear that at least two marked humpback whales were killed in Antarctic area V during the summer of 1961–62. Since marked whales represent only a small fraction of the total catch (in 1959, Australian marks were recovered from 0·9% of the total catch of 2163 humpback whales taken from the group V population), one can infer that a considerable catch (possibly of some hundreds) of humpback whales was taken from Antarctic area V during the summer season of 1961–62.

(*b*) *Natural Mortality and Fishing Mortality Coefficients*

(i) *Group IV Population*

The total mortality coefficient (Z) can be divided into its components, natural mortality (M) and fishing mortality (F), by relating the total mortality to the corresponding fishing effort (f). The total effort was taken as the mean Australian effort in the particular pair of seasons from which the estimate of Z was made, plus the Antarctic effort in the intervening summer (Table 37). The estimates of total mortality (Z) were plotted against the estimated effort (f) for each sex separately (Figs. 29 and 30).

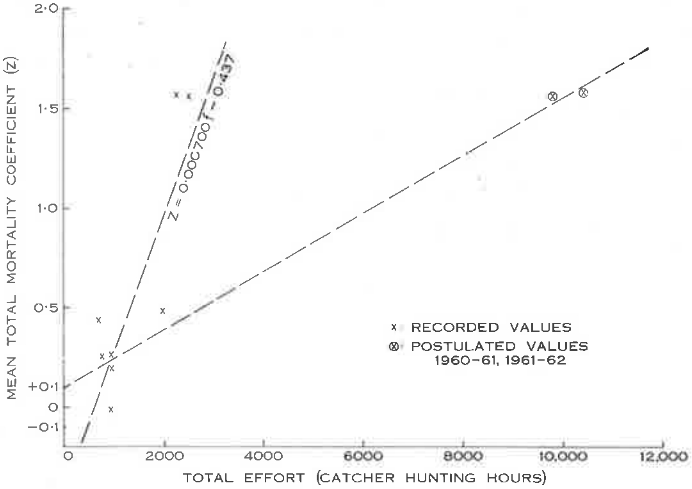

Fig. 31.—Mortality and effort: group V male humpback whales; × recorded values, ⊗ postulated values for 1960–61 and 1961–62.

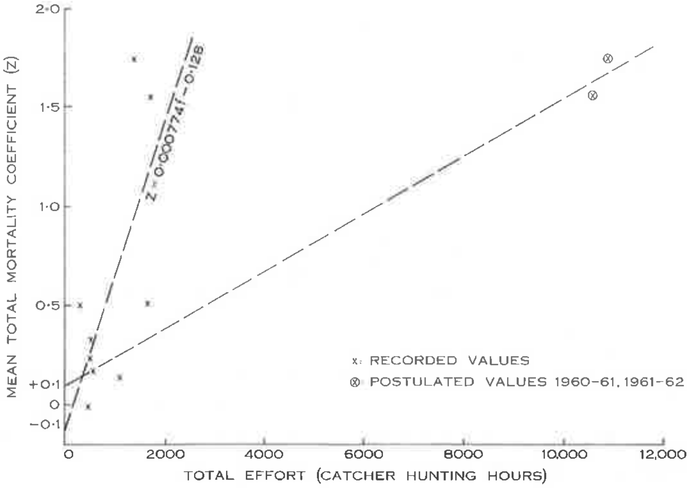

Fig. 32.—Mortality and effort: group V female humpback whales; × recorded values, ⊗ postulated values for 1960–61 and 1961–62.

In each plot the point for 1958–59 was anomalous, the estimated effort being far higher than for any other point, but the total mortality, while high, was not as high as might be expected from the regression. The high effort values derive from very large

Antarctic catches during the summer of 1958–59. If some of these whales did not in fact belong to the group IV population (as indicated by Chittleborough 1959*b*), then the effort as computed would be too high; if 40% of these catches were from outside group IV, then the 1958–59 point would fit closely on the regression line through the other points. For these reasons there appears to be justification in omitting the 1958–59 point from the calculations.

The regressions fitted by least squares, omitting the mortality and effort recorded for 1958–59 gave intercepts on the *y* axis of 0·086 for males and 0·087 for females (standard error 0·140 and 0·129, respectively). These are estimates of the natural mortality coefficient of adult humpback whales from the group IV population.

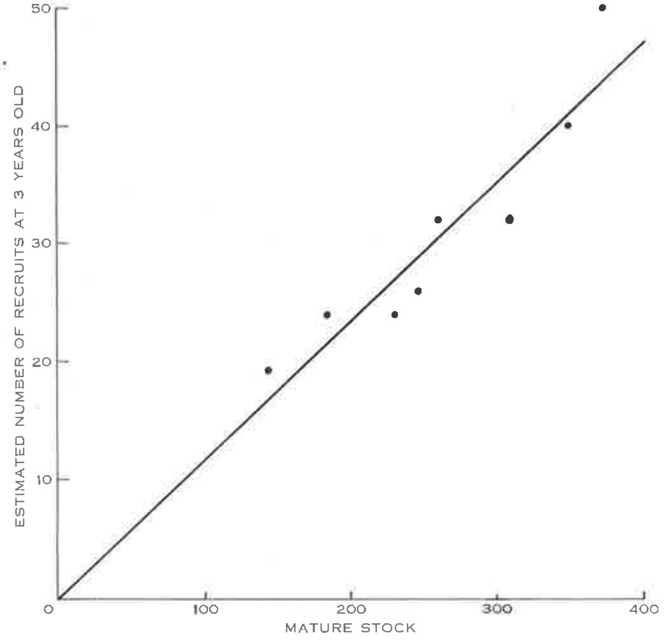

Fig. 33.—Stock–recruitment relationship for group IV humpback whales.

Another approach to the estimation of natural mortality in humpback whales can be made if the age composition has been assessed from a random sample of the virgin stock. This cannot be done in the case of the group IV population because of its previous history of exploitation.

The total mortality in the most recent seasons has ranged from 0·85 to 1·09 for the males and from 0·54 to 0·80 for the females (Table 39). After deducting natural mortality of 0·09, the corresponding fishing mortality coefficients were 0·76–1·00 for males and 0·46–0·71 for females. The difference between males and females is due to the fact that all mature males can be taken by the fishery, while females with calves (35–40% of the total number of mature females) cannot be taken.

(ii) *Group V Population*

The estimates of Z from the data obtained from the east coast of Australia (Table 39) have been plotted against corresponding total effort (Table 38) for each sex separately (Figs. 31 and 32). The regressions fitted by least squares to these points gave intercepts on the y axis of $-0 \cdot 437$ for males and $-0 \cdot 128$ for females. These anomalous values for M were caused by the points for 1960–61 and 1961–62, in which the estimates of effort (based on total reported catch) were far too low in relation to the very high values of Z (the latter being confirmed by independent assessments of mortality from New Zealand catches).

TABLE 41

RECRUITS SURVIVING FROM FEMALES BORN ANNUALLY PER 100 ADULT FEMALES

Female Births (per 100 adult females)	Possible Juvenile Natural Mortality (M)	Survivors to 3 Years of Age	Assumed Natural Mortality in 4th and 5th Years	Recruits, Survivors to 5 Years (maturity)
18·6	0·15	11·9	0·07	10·3
18·6	0·11	13·4	0·07	11·6
18·6	0·07	15·1	0·07	13·1

If the points for the pairs of years 1960–61 and 1961–62 were omitted from the data shown in Figures 31 and 32, significant regression lines could not be fitted to the remaining points as neither total mortality nor effort had changed sufficiently from 1952 to 1959. Then in this case the method of the regression of Z upon f could not be used to separate total mortality into its components (natural and fishing mortality).

Chittleborough (1960*a*) assumed that his estimate of total mortality for adult male humpback whales of the group V population in 1957 and 1958 (based upon samples of ear plugs) was almost unaffected at that time by commercial operations. Then the total mortality coefficient derived from that sample of adult males (0·097) consisted mainly of natural mortality. The estimate of 0·09 for natural mortality for the group IV population should then be regarded as the upper limit for the estimate of M.

If the regression lines of total mortality on total effort for adult males and females in the group V population, are to intercept the y axis at a value of 0·09, approximations can be made for the true positions of the points for 1960–61 and 1961–62 (Figs. 31 and 32). From the difference between the postulated and recorded values of total effort, the additional (unreported) catches in these years can be estimated. On this basis additional mortality within Antarctic area V of some 3700 humpback whales in the summer of 1960–61 and of approximately 1300 humpback whales in 1961–62, would (when added to all other known catches) explain the recent abrupt increase in the total mortality within this stock.

VIII. RECRUITMENT

(*a*) *Stock–Recruitment Relationship*

One approach to the task of estimating recruitment makes use of data on the catch per unit effort from each female age group. The abundance of adult females in each year (from 1949 onwards) on the west coast of Australia has been estimated as the sum of the catches per unit effort of female humpback whales above 5 years of age.

TABLE 42

CATCHABLE STOCK OF GROUP IV HUMPBACK WHALES ESTIMATED FROM CATCH AND FISHING MORTALITY

Year	Australian Catch	Antarctic Catch	Mean Catch	Z	F $(M = 0 \cdot 09)$	Estimated Stock	Australian Catch	Antarctic Catch	Mean Catch	Z	F $(M = 0 \cdot 09)$	Estimated Stock
			Males						*Females*			
1950	250						137					
		468	1047	0·37	0·28	3740		644	868	0·32	0·23	3775
1951	907						310					
		546	1333	0·60	0·51	2615		581	994	0·32	0·23	4320
1952	666						516					
		103	799	0·39	0·30	2665		90	634	0·28	0·19	3335
1953	726						571					
		133	842	0·38	0·29	2905		125	719	0·22	0·13	5530
1954	692						617					
		12	648	0·40	0·31	2095		16	596	0·29	0·20	2980
1955	580						543					
		320	948	0·43	0·34	2790		504	997	0·36	0·27	3690
1956	676						443					
		0	630	0·80	0·71	890		0	488	0·39	0·30	1625
1957	583						536					
		0	546	0·66	0·57	960		0	497	0·37	0·28	1775
1958	509						458					
		645	1065	1·09	1·00	1065		768	1181	0·80	0·71	1665
1959	331						369					
		28	329	0·88	0·79	415		38	360	0·67	0·58	620
1960	271						274					
		3	291	0·85	0·76	385		1	274	0·80	0·71	385
1961	306						272					
		24	329	0·90	0·81	405		32	287	0·54	0·45	635
1962	304						239					

Recruitment to the fishery was taken to occur at 4 years, but since whales were not fully recruited at this age the catches per unit effort of 3-year-old females cannot be used directly, and an indirect method had to be used. This was done for each year class by taking the catches per unit effort at the fully recruited ages, and converting these to actual numbers in the population using the relation that a catch per unit effort of 0·1 is equivalent to a population of 2000 whales (see Section IX (*a*)). The numbers of 3-year-old females was then estimated by adding the known catches of females in the year class, and the estimated deaths by natural mortality (assuming $M = 0 \cdot 1$, but this value is not a critical one).

The estimated number of recruits (3 years old) in each year was then plotted against the number of females in the parent generation, i.e. the number of adult females 4 years earlier (i.e., the pregnant females of 1950 give birth in 1951 and these are the 3-year-old recruits in 1954). The result is shown in Figure 33, giving the relationship R (recruits) $= 0\cdot12 \times$ mature stock. Annual recruitment (of 3-year-old whales) as measured by this method is then 12 females per 100 adult females.

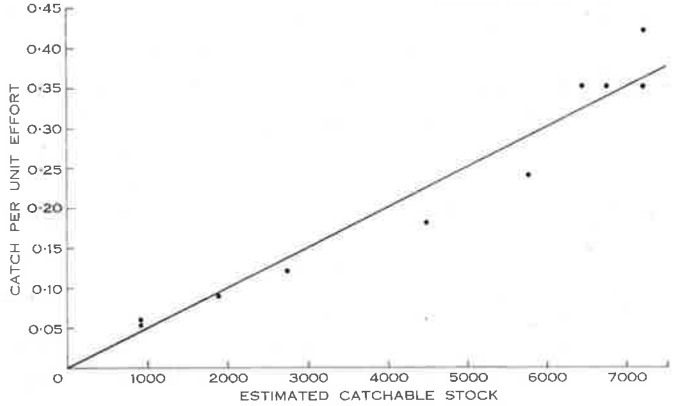

Fig. 34.—Relationship between catch per unit effort and catchable stock size as estimated from catch and fishing mortality; group IV population.

(*b*) *Estimates of Recruitment from Pregnancy Data*

A more direct measure of recruitment can be made by applying juvenile mortality to the birth rate, if these values can be determined. In order to measure the latter, attempts have been made to distinguish in the ovaries, corpora albicantia of previous pregnancies from those of ovulations which had not resulted in pregnancy, but as discussed in Section III (*a*)(iv), these attempts have been unsuccessful.

Since there is a seasonal breeding cycle, and the gestation period is almost 12 months long, the proportion of mature females carrying near-term foetuses during the northward migration (when all mature females are equally vulnerable), gives a measure of the birth rate in this population. Using this method with the data from the whaling station at Albany, the average annual birth rate was found to be 0·372 (Section III (*a*)(iv)).

Nishiwaki (1959) used a somewhat similar method to estimate the birth rate of humpback whales in Aleutian waters. He found that approximately 65% of the mature female humpback whales available for catching were pregnant. Since lactating females were not vulnerable, and as equal numbers of lactating and pregnant females could be expected, the composition of the mature female stock feeding in Aleutian waters during the summer should be 65 pregnant : 65 lactating: 35 resting females. This is equivalent to an average annual birth rate of 0·39.

The estimate from the data collected at Albany is more precise than that of Nishiwaki, as the former was based on samples of all categories of mature females, weighted according to the fishing effort applied throughout the northward migration past that sampling point.

If the birth rate is 0·372 and the sex ratio at birth is 0·5, then 100 mature females will give birth to 18·6 female calves per year. The number of 3-year-old female recruits is therefore: $18{\cdot}6e^{-3M}$ where M is the average natural mortality in the first 3 years. Natural mortality of juveniles has not been measured but it is almost certainly greater than adult natural mortality. A likely range of values for juvenile mortality and the resultant survivors to 3 years of age are shown in Table 41. From the estimate of recruitment at 3 years of age derived from the stock–recruitment relation in the previous section (12 per 100 adults) juvenile mortality would apparently lie in the upper part of the range given in Table 41.

TABLE 43

ESTIMATES OF POPULATION SIZE OF GROUP IV HUMPBACK WHALES BY VARIOUS METHODS

Year	Estimated Catchable Population (from mortality rates)	Catch per Unit Effort	Estimated Catchable Population (from catch per unit effort)	Estimated Catchable Population (DeLury)	Estimated Total Population (sightings)
1930's					10,200
1950		0·47	9400		
1951	7225	0·42	8400		
1952	6450	0·35	7000		
1953	7220	0·35	7000		
1954	6755	0·35	7000		
1955	5775	0·24	4800	9800	
1956	4495	0·18	3600	7800	
1957	2625	0·15	3000	6700	
1958	2730	0·12	2400	5600	
1959	1880	0·09	1800	3700	
1960	905	0·06	1200	2900	
1961	905	0·055	1100	2400	
1962		0·05	1000	1800	

Although some whales are taken by the catchers when 3 years of age, females are not mature until, on the average they are 5 years old. Assuming natural mortality during their fourth and fifth years to be 0·07 (though 0·09 has little effect on the result), recruitment (to maturity) may range from 0·10 to 0·13 (Table 41).

IX. Population Size

(a) Group IV Population

A first approximation of population size can be derived from data of sightings of baleen whales in the southern hemisphere in 1933–39. From these records Mackintosh and Brown (1956) estimated a total baleen whale stock of 220,000–340,000, the larger figure being the more likely. Mackintosh (1942) had previously estimated that 10% of the larger baleen whales in the southern hemisphere were humpbacks so that in the 1930's the southern humpback whale populations may have contained some 22,000–34,000 individuals. These have to be apportioned between the five distinct populations. Following the guide given by Mackintosh (1951), a fair measure of the relative abundance within the populations during the 1930's is as follows:

Group I	Group II	Group III	Group IV	Group V
1	1	2	3	3

Thus, if the group IV population included 30% of the total southern stocks of this species in the 1930's this population contained from 6600 to 10,200 humpback whales, the larger figure being probably the more likely.

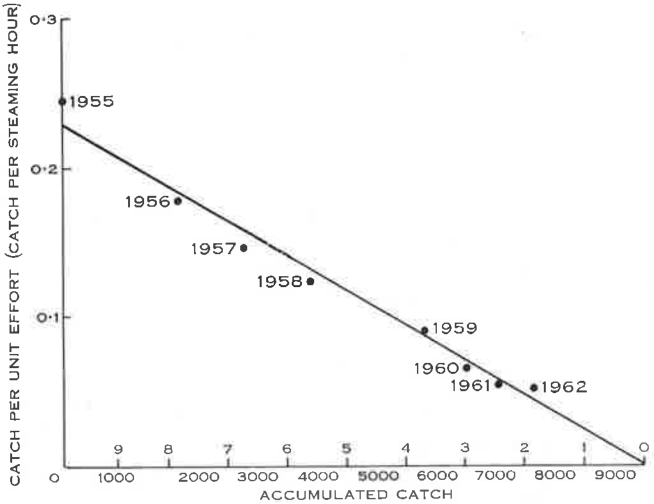

Fig. 35.—DeLury method on group IV population of humpback whales.

The average population size during each recent season can be estimated directly from the catch data and the estimates of fishing mortality (*F*), as shown in Table 42. The upper limit of M (0·09) has been used; lower values for natural mortality decrease the estimates of stock size only slightly. These estimates refer to catchable stocks of males and females.

The regression of catch per unit effort (best estimate) on total catchable stock is a straight line (Fig. 34) on which a catch per unit effort of 0·1 is equivalent to 2000 humpback whales in the catchable stock. The population sizes estimated from this relation are shown in Table 43.

Another independent estimate of stock size has been obtained from the DeLury (1947) method of plotting catch per unit effort against accumulated catch. This gives a very good relation for the data since 1955 (Fig. 35), with an intercept on the x axis of 9800 ± 1100, which is an estimate of the catchable stock in 1955. However, this method gives biassed estimates because no allowances have been made for recruitment, natural mortality, the effects of migration, etc. The errors resulting from neglect of these factors leads to an overestimate of the population size.

The various estimates of group IV population size are shown together in Table 43. Unfortunately, the estimate from sightings cannot be compared directly with those by other methods because the period covered by the sighting records does not overlap that to which the other data refer. The history of whaling on this stock (Section IV) is of few catches before 1934, very heavy catches (12,673 in all) from 1934 to 1939, and no whaling from 1939 to 1949. Thus, the stock in 1939 was probably considerably less than the 1950 stock, and the population in 1934 much more than that in 1939 (by an amount less than 12,000 whales). If the population size had been 9400 in 1950, and if over the previous 11 years (when there had been no fishing mortality) the rate of increase ($r-M$) had been within the range of values given in Section X(*a*), the 1939 population was somewhere in the range of 4000–8000. The 1934 population would then have been in the range of 12,000–16,000. The sighting estimate of 10,000 humpback whales in this population during the period 1933–39 fits well inside this range.

TABLE 44

MEAN CATCHABLE STOCK OF GROUP V HUMPBACK WHALES ESTIMATED FROM CATCH AND FISHING MORTALITY

Period	1952–59	1959–60	1960–61	1961–62
Mean total mortality (Z)	0·224	0·50	1·56	1·67
Fishing mortality (F) ($M = 0{\cdot}09$)	0·134	0·41	1·47	1·58
Annual catch (C)	1329*	2241*	1456* 5156†	595* 1895†
Mean population size (C/F)	9920*	5470*	990* 3510†	380* 1200†

* Total reported catches.

† Assuming additional mortality of 3700 humpback whales in 1960–61 and of 1300 in 1961–62.

The best estimate of the mean catchable stock in 1962 is that it consisted of 1000 whales. In order to determine the number left at the end of 1962, the estimate of mean stock size should be reduced by approximately half the catch taken on the west coast of Australia during the winter season of 1962. Even allowing for some recruitment, the total number of catchable whales remaining in the group IV population at the end of 1962 would not exceed 800.

(*b*) *Group V Population*

The population estimates from sightings (described in the previous section) suggest that the group V humpback whale population contained approximately 10,000 individuals in the period 1935–39. Since there had been little previous exploitation of this population, this estimate is of the size of the population in the virgin state.

Estimates of the size of the catchable stock in recent years, made from fishing mortality coefficients and total catch data (Table 44), suggest that its mean size between 1952 and 1959 was similar to that of the population between 1933 and 1939 as calculated from sightings. There had been little fishing of this population from 1939 to 1950, and the population had apparently remained stabilized.

Since 1959 the population has diminished rapidly. If the total catches were as reported to the Bureau of International Whaling Statistics, the catchable stock remaining at the end of 1962 was less than 200 humpback whales. However, if as suggested in Section VII (*b*), the catches were understated by 3700 humpbacks in 1960–61 and by 1300 in 1961–62, the catchable stock left at the end of 1962 was close to 500 whales.

The method of DeLury was used to obtain independent estimates of the upper limits of population size in recent years. From the regression of catch per unit effort on the accumulated catch from all known records, fitted to the data from 1959, 1960, 1961, and 1962 (Fig. 36), the upper limit of the population size in 1959 would have been 4600 humpback whales. Since the DeLury method must overestimate the population size (especially when used with data such as are available here) this estimate for 1959, being less than the estimate from catch and fishing mortality data (Table 44), is unacceptable.

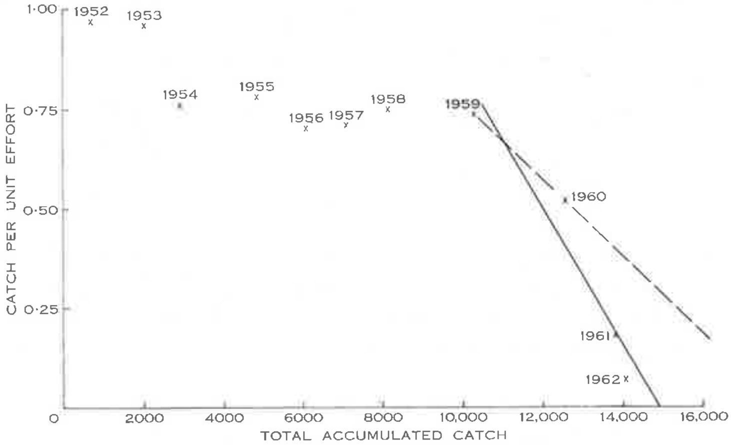

Fig. 36.—Group V population: catch per unit effort and cumulative catch.

If in Figure 36 the regression line is taken only through the values for 1959 and 1960, the intercept on the *x* axis gives an estimate of the population size in 1959 of 7600 humpback whales. This second regression would require that approximately 4900 more humpback whales had been taken in 1961 and 1962: this value is very close to the estimate that 5000 more humpback whales must have been killed in the summers of 1960–61 and 1961–62, to account for the very high mortality coefficients in those years (Section VII (*b*)(ii)).

X. Stock Assessment

(*a*) *Group IV Population*

The net rate of change of the population is the difference between *r* (the recruitment coefficient) and the sum of *F* (the fishing mortality coefficient) and *M* (the natural mortality coefficient). The population will be in balance, neither increasing nor decreasing if $F = r - M$, and the catch taken is $F \times P = (r-M)P$, where P is the mean population size. Either, or both, M and r will change with population size, M increasing and r decreasing, or M remaining stable and r decreasing, or M increasing and r remaining unchanged as the population increases, and when the population is at its maximum, in the unfished state, $M = r$. The exact relation of M and r is difficult to determine but some reasonable assumptions can be made, and hence the form of the curve $c = (r-M)P$ giving the steady yield determined, and in particular the position and height of the maximum estimated.

For the stock sizes of recent years, r has been estimated (Table 41) as $0{\cdot}116$, and the reasonable limits given as $0{\cdot}10$ and $0{\cdot}13$. The upper limit of M was found to be $0{\cdot}09$ (Section VII (*b*)), the best estimate being $0{\cdot}07$, while the data are also consistent with a value of $0{\cdot}05$.

A range of values of r–M can now be given as follows:

Best estimate $0{\cdot}116-0{\cdot}07 = 0{\cdot}046$,
High estimate $0{\cdot}13-0{\cdot}05 = 0{\cdot}08$,
Low estimate $0{\cdot}10-0{\cdot}09 = 0{\cdot}01$.

The total (catchable) population remaining at the end of 1962 was around 800 whales of which not more than half were adults (Table 32). Taking the mature population as 400 whales, the catches that could be taken from this population without causing a further decline are:

Best estimate $400 \times 0{\cdot}046 = 18$,
High estimate $400 \times 0{\cdot}08 = 32$,
Low estimate $400 \times 0{\cdot}01 = 4$.

Therefore, some 18 whales could be taken per year, and the stock would maintain itself at the present level. Almost certainly if more than 32 whales were taken the stock would decline.

The size of the stock of humpback whales in the unfished state is not known accurately but before 1949 the catches taken from it were 5800 in 1912–16, 3400 in 1925–28, and 12,800 in 1934–39. Assuming that the stock had recovered to some extent between these periods of whaling, the unfished population was probably between 12,000 and 17,000. In this presumably stable population $r-M=0$, so that as the stock approaches its maximum size there must be a critical reduction in r, or an increase in M, or both.

The maximum sustainable catch therefore probably comes from a stock level of around 10,000 humpback whales, which is about the level in 1949. In this population 85% were mature, so that the maximum sustainable yield is estimated as follows:

Best estimate $8500 \times 0{\cdot}046 = 391$,
High estimate $8500 \times 0{\cdot}08 = 680$,
Low estimate $8500 \times 0{\cdot}01 = 85$.

The calculation of these permissible catches has been based on data relating to the mature stock, with the assumption that the catch would be taken only from the mature segment of the population. The result would have been much the same if the assumption were made that the catch would be drawn from both mature and immature whales. Catches of immature whales would tend to reduce the net rate of recruitment to the mature part of the stock, and hence the sustainable catch from mature whales. However, allowing for the fact that under this regime, some of the whales that would die from natural causes before reaching maturity are captured, the sustainable catch in numbers would be very slightly increased by fishing both mature and immature segments of the population. On the other hand, the sustainable catch in weight will be slightly less if both mature and immature whales are taken.

If the populations were to be conserved by operating each year on the maximum sustainable yield, the minimum legal length could be abolished. As suggested by Ruud (1954) the application of size limits in whaling may have done more harm than good.

The time taken for the stock to build up to the optimum level can be estimated from the potential net rate of increase, $r-M$. If whaling on the group IV population had been stopped at the end of 1962 there would have been an initial rather rapid increase in the mature stock because of recruitment from the larger mature stocks present in 1958 and 1959 (which now form the dominant immature stock). The mature stock in 1964 would therefore have been about 900 (allowing for some loss, because of natural mortality, of whales now in the stock). These 900 would then increase at a rate of $r-M$, and reach the 8500 level after T years, where

$$\mathrm{e}^{(r-M)T} = 8500/900,$$

i.e. $(r-M)T = 2{\cdot}25$. Using the best estimate of $r - M$ ($0{\cdot}046$), $T = 49$ years; using the high estimate of $r-M$ ($0{\cdot}08$), $T = 28$ years.

The length of this delay period is critically dependent upon the level to which the population is reduced before whaling is stopped. If whaling had been stopped in 1959, when the catchable stock was about 1800, then the mature stock after 2 years would have been about 1620, and

$$\mathrm{e}^{(r-M)T} = 8500/1620,$$

i.e. $(r-M)T = 1{\cdot}66$, $T = 36$ years (best estimate), or 21 years (high estimate of $r-M$).

Conversely, if whaling continued at the present level, the mature stock would decline at the rate of $F-(r-M)$, which is about $0{\cdot}7$. That is, each year that whaling continued at the present level in terms of fishing mortality rate (the actual numbers taken would decline proportionately to the stock) would increase the delay, until the stock can recover to its optimum level, by at least $0{\cdot}7/0{\cdot}08 = 8{\cdot}8$ years, and probably by $0{\cdot}7/0{\cdot}046 = 15$ years. In terms of catch lost at the optimum level these delays are equivalent to $8{\cdot}8 \times 680 = 5984$ whales, or $15 \times 391 = 5865$ whales. The actual estimate is therefore very little affected by the precise estimate of $r-M$: a long delay period, due to a low value of $r-M$, corresponds to a lower catch at the optimum stock level. This figure of the net loss of 6000 from the potential catch for each year that operations are continued, may be compared with the actual catch in 1962 of 543 whales.

(*b*) *Group V Population*

Pregnancy rates recorded from Cook Strait, N.Z., from 1948 to 1962 were almost identical with those recorded in recent years from Albany (west coast of Australia), so a similar value for recruitment applies to both populations. Natural mortality also appears to be the same in the two populations, so that the range of values for $r-M$ given for the group IV population will be applied to the assessments upon the group V stock.

The total catchable stock remaining at the end of 1962 was close to 500 humpback whales. The mature population, therefore, was about 260 (52% of the 1962 catch were mature). The catches that could be taken from this population without causing a further decline were:

Best estimate	$260 \times 0{\cdot}046 = 12,$
High estimate	$260 \times 0{\cdot}08 = 21,$
Low estimate	$260 \times 0{\cdot}01 = 3.$

Virtually any commercial catches from this population would reduce the stock below the present extremely low level. Hunting of this population in temperate latitudes has now ceased, so that provided these whales are not molested in Antarctic area V, the population may recover at the rate of $P.\mathrm{e}^{(r-M)T}$.

The size of the original population was in the region of 10,000 humpback whales, whereas the maximum sustainable catch probably comes from a stock level of about 8500, and if 85% were mature, this means an adult stock of 7225 whales. The maximum sustainable yield would then have been:

Best estimate	$7225 \times 0{\cdot}046 = 332,$
High estimate	$7225 \times 0{\cdot}08 = 578,$
Low estimate	$7225 \times 0{\cdot}01 = 72.$

If there is no further hunting of this population the mature stock size will be increased initially by the recruits from the larger population present in 1958 and 1959. However, the paucity of sightings during the 1962 season suggests that these juveniles had also suffered heavy mortality, so that the mature stock cannot be expected to gain greatly from these recruits. The mature stock in 1964 may be no more than 400 whales. This stock would reach 7225 after T years, so that:

$$\mathrm{e}^{(r-M)T} = 7225/400,$$

$$(r-M)T = 2{\cdot}89.$$

If $r-M = 0{\cdot}046$, then $T = 63$ years; if $r-M = 0{\cdot}08$, then $T = 36$ years.

The best estimate of the period of protection necessary for the population to recover to the level required for the maximum sustainable yield is then 65 years, and the most optimistic figure at least 38 years.

As the period needed for full recovery is so great, a whaling station might desire to operate on a smaller scale after a shorter period of protection. An annual catch of say 150 humpback whales would require a mature stock of 3260 whales. If the mature stock size was 400 in 1964, the time taken to reach a level of 3260 adults would be 46 years if $r-M = 0{\cdot}046$ (best estimate) or 19 years if $r-M = 0{\cdot}08$.

XI. Present Status of Fishery

The group IV and V populations of humpback whales are now so depleted that neither will support commercial operations relying solely on this species.

After the failure of the humpback whale fishery in 1962, the whaling stations at Tangalooma, Byron Bay, and Norfolk I., were closed down indefinitely, while the station in Cook Strait, N.Z., has turned to sperm whaling. Thus the group V population of humpback whales was afforded some measure of protection, at least in the northern part of its range.

On the west coast of Australia the station at Albany has depended mainly on sperm whales for several years, although some humpback whales continue to be taken. The station at Carnarvon has entered into other fishing as well as exploring the prospects of sperm whaling, while continuing to hunt humpback whales. In 1963 the Australian Government issued quotas of 450 humpback whales to the station at Carnarvon, and 100 to the station at Albany. Both stations discontinued hunting humpback whales in August owing to scarcity of whales; total catches were 68 humpback whales at Carnarvon, and 19 at Albany.

In July, 1963, the International Whaling Commission passed a resolution that humpback whaling should cease in the southern hemisphere. If this resolution can be put into effect, the group IV and V populations of humpback whales will recover within the range of rates set out above.

XII. Acknowledgments

A large portion of the data and material used in this paper was collected at whaling stations by various members of the Division of Fisheries and Oceanography, CSIRO, as well as by Commonwealth and State whaling inspectors. Australian whaling companies cooperated closely, making facilities available at whaling stations, keeping special records of effort and sightings on catchers and aircraft, giving the author access to ships' logs, and by marking whales when opportunities occurred.

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PRELIMINARY ASSESSMENTS OF STOCKS OF THE WESTERN AUSTRALIAN CRAYFISH, *PANULIRUS CYGNUS* GEORGE

By B. K. Bowen* and R. G. Chittleborough†

[*Manuscript received July* 6, 1965]

Summary

Total catch of *Panulirus cygnus* in Western Australia rose from 0·6 million lb in 1944–45 to 21·4 million lb in 1962–63. Fishing effort increased rapidly with the result that the catch per unit effort declined progressively. Effort has been limited by regulation since 1963.

From records of catch and effort from specified areas at intervals of one month throughout each season, estimates were made of mortality coefficients (Z^1, F, and M^1) and catchability coefficient (q). Stock size, recruitment, and exploitation rates were then estimated. As the seasonal catch per unit effort followed the same trend throughout all fishing areas, the detailed results from the selected areas have been applied to the whole fishery.

The fishable stock, originally of approximately 140 million lb, had declined to some 35 million lb by 1963. Exploitation rate rose as effort was increased, and then levelled off (generally at above 60%), further increase in fishing effort resulting in a fall in the catchability coefficient rather than a change in the exploitation rate. Because of the high exploitation rate in recent years, the fishable stock available on the grounds at the opening of a season is largely dependent on recruitment (by growth) of juveniles during the preceding closed period. This recruitment has been diminishing from year to year, apparently because of mortality of undersize (pre-recruit) crayfish handled in fishing pots. Provision of escape gaps in all fishing pots is recommended.

A sustainable level of catch might be 16,000,000±2,000,000 lb per year if recruitment can be stabilized. Some further restriction of fishing effort might be necessary.

I. Introduction

The Western Australian crayfish, *Panulirus cygnus*, occurs on the west coast of Australia from North West Cape (21°45′S.) to Cape Leeuwin (34°22′S.), being concentrated on coastal reefs. Some are taken down to 80 fm. Formerly regarded as a discrete population of *P. longipes*, it was described as a new species by George (1962).

The commercial fishery can be divided into two major areas (Fig. 1); the coastal area, from 28 to 33°S., is opened on November 15 each year and remains open until August 15 of the following year; the Abrolhos area has an open season extending from March 15 to August 15. There have been some variations of the period of open season in earlier years as reviewed by Sheard (1962).

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Figure 2 illustrates the development of the fishery in post-war years, the total commercial catch rising from 0·6 million lb in 1944–45 to 21·4 million lb in 1962–63. Until 1963 there were no restrictions on fishing effort, the number of men, boats, and pots per boat increasing steadily each year as given in detail by Sheard (1962). During 1963 the Western Australian Government limited the number of boats operating in the crayfish industry, and the number of pots per boat. Since March 1, 1963, the number of crayboat licenses available has remained constant, and from November 15, 1963, the number of pots per boat was limited to three per registered foot of boat length with a maximum of 200 pots. Some of the larger vessels were not affected by the regulation, whereas many of the smaller boats had to reduce their number of pots

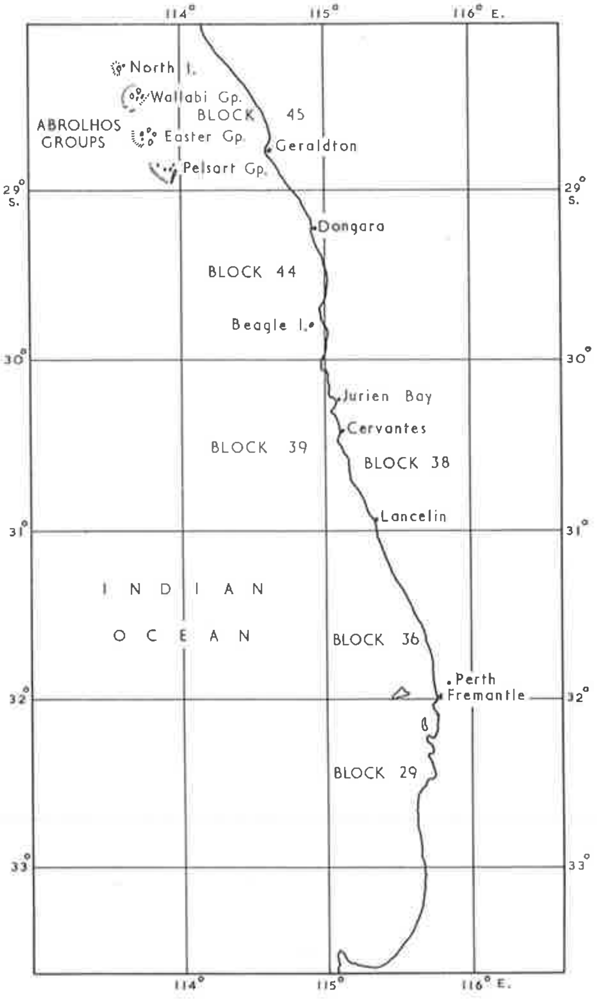

Fig. 1.—Map showing crayfishing areas of Western Australia.

by as much as 50%. As a result, the total number of pots fishing in 1963–64 was approximately 78% of that of the previous season.

These restrictions were imposed upon fishing effort because of the very rapid increase in the number of pots used in this fishery during recent years, without a corresponding increase in catch. Indications of decline in catch rate in some areas, supported by reports from fishermen, showed that a detailed assessment of the crayfish stock and of the effects of the present level of exploitation, was urgently needed.

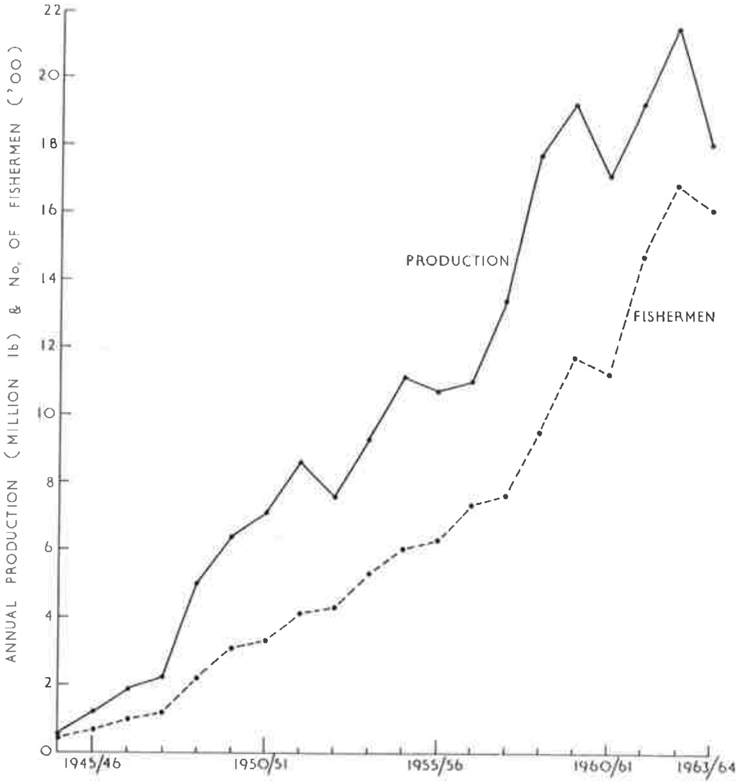

Fig. 2.—Annual production of crayfish in Western Australia (●—●), and number of fishermen operating (●- - -●).

Reasonably complete records of catch and effort are available since the early years of the fishery (though not always in as much detail as one would wish). However, quantitative biological data upon reproduction, growth, natural mortality, migration, etc., were very limited, indeed sometimes non-existent.

Preliminary assessments of stock, recruitment, and exploitation rates were derived from the catch and effort data so that conservation measures could be reviewed as early as possible. The ecological and other biological studies required for a proper understanding of the processes within this population are being carried out so that more precise estimates can be made of stock size and sustainable yield.

TABLE 1

COMMERCIAL CATCH AND EFFORT FOR EACH MONTH AT THE EASTER GROUP (INNER AREA, ABROLHOS) 1950–64

Catches (*c*) are given in thousands of pounds weight and effort (*g*) in thousands of pot-nights

Year	Statistic	March	April	May	June	July	August
1950	Catch (*c*)	—	217·1	154·9	122·8	109·0	86·6
	Effort (*g*)	—	21·2	22·7	24·8	18·7	14·7
	c/*g*	—	10·24	6·82	5·00	5·84	5·90
1951	Catch (*c*)	—	174·0	153·5	65·8	82·0	70·2
	Effort (*g*)	—	18·2	18·8	16·2	14·6	14·6
	c/*g*	—	9·5	8·2	4·1	5·6	4·8
1952	Catch (*c*)	—	163·9	145·0	88·0	100·7	82·2
	Effort (*g*)	—	24·8	24·9	25·6	23·3	21·8
	c/*g*	—	6·6	5·8	3·4	4·3	3·8
1953	Catch (*c*)	88·5	219·1	143·2	66·9	96·0	34·2
	Effort (*g*)	15·8	34·7	36·7	27·4	33·4	14·0
	c/*g*	5·60	6·31	3·90	2·44	2·90	2·45
1954	Catch (*c*)	156·4	279·8	178·8	62·9	102·1	34·7
	Effort (*g*)	19·5	42·9	36·1	30·8	28·4	10·8
	c/*g*	8·02	6·52	4·96	2·04	3·60	3·22
1955	Catch (*c*)	156·5	185·7	95·0	46·7	96·0	37·7
	Effort (*g*)	24·6	40·6	37·0	29·8	37·9	10·4
	c/*g*	6·36	4·58	2·56	1·57	2·53	3·62
1956	Catch (*c*)	86·2	260·1	165·4	41·8	76·0	*
	Effort (*g*)	16·2	36·2	48·2	28·4	28·9	
	c/*g*	5·31	7·18	3·43	1·47	2·63	
1957	Catch (*c*)	170·4	262·7	166·1	39·2	106·5	19·3
	Effort (*g*)	25·9	49·0	50·6	31·7	36·2	10·2
	c/*g*	6·60	5·40	3·30	1·24	3·00	1·90
1958	Catch (*c*)	181·3	309·6	159·5	57·0	85·9	30·3
	Effort (*g*)	27·0	61·6	52·5	41·0	49·7	13·8
	c/*g*	6·71	5·03	3·04	1·40	1·73	2·20
1959	Catch (*c*)	175·7	262·9	133·1	53·9	61·7	18·2
	Effort (*g*)	28·4	71·5	59·2	46·9	43·1	9·5
	c/*g*	6·19	3·68	2·25	1·15	1·43	1·91
1960	Catch (*c*)	305·2	199·0	111·8	63·0	45·6	21·4
	Effort (*g*)	80·0	67·7	70·2	56·5	54·7	22·7
	c/*g*	3·82	2·94	1·60	1·12	0·83	0·94
1961	Catch (*c*)	299·7	166·1	86·9	40·6	29·6	11·6
	Effort (*g*)	91·5	66·5	54·4	44·0	28·2	12·3
	c/*g*	3·28	2·50	1·60	0·92	1·05	1·00

* Records not available.

Table 1 (*Continued*)

Year	Statistic	March	April	May	June	July	August
1962	Catch (*c*)	316·9	196·9	92·5	38·7	54·8	18·4
	Effort (*g*)	98·4	78·8	73·6	51·7	58·0	15·9
	c/*g*	3·22	2·50	1·27	0·75	0·94	1·16
1963	Catch (*c*)	294·9	157·3	79·4	37·1	54·2	31·6
	Effort (*g*)	134·0	111·2	99·6	71·7	79·7	23·6
	c/*g*	2·20	1·41	0·80	0·52	0·68	1·34
1964	Catch (*c*)	135·8	225·0	98·3	39·1	40·2	*
	Effort (*g*)	42·9	84·4	64·2	50·4	52·9	
	c/*g*	3·17	2·67	1·53	0·78	0·76	

* Records not available.

II. Source of Data

The catch and effort data have been taken from the Western Australian Department of Fisheries and Fauna records. Some of these data have been listed by Sheard (1962).

At the Abrolhos area the catch has been recorded for each of the three major island groups, i.e. Pelsart, Easter, and Wallabi (including North I.). Each group has been further divided to give the catch on the shallow grounds within the reef system (inner areas), and on the deep water grounds outside the reefs (outer areas). The total catches (in pounds weight) from these areas have been recorded for each month of fishing.

Information upon fishing effort expended has been variously recorded in terms of the number of boats, men, or pots, or both operating in each block or area during each month. The most satisfactory unit of effort is the crayfish pot fishing for one unit of time. Since pots are normally pulled each day, the ideal unit of effort is a pot fishing for one night. However, before 1964 the statistical returns submitted by fishermen did not indicate the number of days during the month on which they actually pulled their gear. For the purpose of the present analysis it has been assumed that all pots were pulled each day of the month. Since in practice the weather conditions do not allow the gear to be pulled daily, total effort (pot-nights) will be an overestimate and the catch per pot-night correspondingly underestimated. However, these errors should be of the same order of magnitude each year and any trends in the catch per pot-night will reflect actual trends in the density of crayfish.

Tables 1–3 show the catch and effort for each month of the fishing season from 1950 to 1964, at the inner areas of the three island groups at the Abrolhos. No record was made of the number of pots fished prior to 1950. For the earlier years, gross estimates of total effort expended during each season were made using the recorded number of men or boats fishing, the average number of pots operated per man or boat, and the number of days in the season. Table 4 shows the total catch and effort expended each year on the outer areas of the three island groups since fishing extended outside the reefs from 1955.

TABLE 2

COMMERCIAL CATCH AND EFFORT FOR EACH MONTH AT THE PELSART GROUP (INNER AREA), ABROLHOS 1950–64

Catches (c) are given in thousands of pounds weight and effort (g) in thousands of pot-nights

Year	Statistic	March	April	May	June	July	August
1950	Catch (c)	—	248·9	193·5	127·1	102·1	136·7
	Effort (g)	—	24·2	28·2	20·3	23·7	19·3
	c/g	—	10·25	6·87	6·28	4·32	7·10
1951	Catch (c)	—	171·8	170·0	44·3	65·8	50·2
	Effort (g)	—	25·2	24·2	21·0	19·9	?
	c/g	—	6·82	7·03	2·11	3·38	
1952	Catch (c)	—	142·1	114·9	52·1	41·8	44·4
	Effort (g)	—	22·5	23·3	18·8	12·4	7·7
	c/g	—	6·32	4·94	2·78	3·38	5·77
1953	Catch (c)	51·6	129·9	72·4	17·7	11·7	10·7
	Effort (g)	9·3	21·6	19·8	12·5	5·2	2·6
	c/g	5·54	6·01	3·67	1·42	2·28	4·12
1954	Catch (c)	72·2	127·7	107·5	38·3	51·4	15·7
	Effort (g)	8·2	18·1	18·4	12·3	12·2	4·1
	c/g	8·77	7·07	5·86	3·12	4·23	3·80
1955	Catch (c)	105·1	132·8	74·9	31·5	63·4	13·8
	Effort (g)	21·7	22·5	16·9	19·1	33·9	4·6
	c/g	4·85	5·91	4·43	1·66	1·87	3·01
1956	Catch (c)	65·7	133·1	116·5	39·0	36·5	33·0
	Effort (g)	10·2	24·8	42·0	27·5	21·0	7·0
	c/g	6·43	5·36	2·78	1·42	1·74	4·74
1957	Catch (c)	66·4	101·8	88·9	15·8	60·8	5·0
	Effort (g)	11·2	23·4	32·7	10·8	21·7	3·3
	c/g	5·91	4·35	2·72	1·47	2·80	1·50
1958	Catch (c)	56·5	97·5	77·5	24·3	31·2	3·3
	Effort (g)	10·6	22·6	21·6	13·7	14·4	3·5
	c/g	5·32	4·31	3·58	1·77	2·17	0·95
1959	Catch (c)	42·8	131·9	60·0	14·2	27·0	10·0
	Effort (g)	7·4	27·9	23·8	15·3	12·9	4·1
	c/g	5·77	4·73	2·52	0·93	2·01	2·45
1960	Catch (c)	77·9	126·0	51·7	32·0	27·9	12·9
	Effort (g)	26·2	30·7	22·2	22·4	20·7	8·9
	c/g	2·97	4·11	2·33	1·43	1·35	1·44
1961	Catch (c)	166·9	107·3	34·2	14·8	16·2	8·5
	Effort (g)	30·7	30·7	16·3	14·1	13·0	6·0
	c/g	5·43	3·50	2·10	1·05	1·25	1·41

Table 2 (*Continued*)

Year	Statistic	March	April	May	June	July	August
1962	Catch (*c*)	147·2	115·6	54·9	19·6	27·4	9·6
	Effort (*g*)	40·9	33·7	29·0	25·0	25·8	11·7
	c/*g*	3·60	3·43	1·90	0·75	1·06	0·82
1963	Catch (*c*)	156·9	103·0	47·0	13·2	27·9	16·2
	Effort (*g*)	44·1	47·2	48·5	26·5	26·2	11·2
	c/*g*	3·56	2·18	0·91	0·50	1·07	1·44
1964	Catch (*c*)	64·3	109·7	58·3	8·3	12·5	*
	Effort (*g*)	17·7	30·1	26·3	14·6	14·6	
	c/*g*	3·63	3·65	2·22	0·57	0·86	

* Records not available.

For the coastal fishery catch and effort have been recorded in statistical blocks measuring 1 degree of latitude by 1 degree of longitude as shown in Figure 1. The coastal fishery is composed of two distinct parts; the "red" fishery from January to August (Table 5), and the "white" fishery upon newly moulted immature crayfish in November–December (Table 6).

Ideally, the catch and effort data for each period of time should relate to small areas where the density of crayfish is uniform and the whole area has been accessible throughout the period of commercial fishing. This is probably more or less the situation in the inner areas of the Abrolhos island groups but it does not apply to the outer areas or to the coastal statistical blocks. There is little doubt that considerable expansion has taken place over the years in any one block. Therefore, the average catch per unit of effort per block from one year to the next does not necessarily apply to the same area of ground. This may not be as serious as it may first appear because it is likely that fishermen expanded into new areas only when the catch per pot-night was reduced to approximately the same level as the ground into which they expanded.

Both the fishing power and the catchability coefficient of the crayfish pot may alter during the history of a fishery, thereby altering the effect of a unit of effort. The catchability has decreased in recent years as a result of an increase in the number of pots used. This could be manifest in several ways. Firstly, as each fisherman endeavours to use more and more pots, his efficiency in setting each pot decreases. He may even set pots on sand, when fishing for red crayfish, because he does not have sufficient time to find suitable ground, or he may allow legal-size crayfish to escape by neglecting to repair damaged battens on his pots. Secondly, the density of pots per unit area may create inter-pot competition, which reduces the effectiveness of each pot. Thirdly, a fisherman operating a large number of pots may, by being unable to pull all pots every day, again reduce the effectiveness of each unit of effort.

III. Abrolhos, Inner Areas

(*a*) *Treatment of Data*

The only reasonably well-circumscribed areas, where fishing does not spread progressively through regions of different density of crayfish (and depth of water),

TABLE 3

COMMERCIAL CATCH AND EFFORT FOR EACH MONTH AT THE WALLABI GROUP AND NORTH I. (INNER AREAS, ABROLHOS) 1950–64

Catches (*c*) are given in thousands of pounds weight and effort (*g*) in thousands of pot-nights

Year	Statistic	March	April	May	June	July	August
1950	Catch (*c*)	—	205·9	129·4	88·1	79·0	112·1
	Effort (*g*)	—	26·2	25·4	19·9	21·7	14·9
	c/*g*	—	7·87	5·09	4·43	3·64	7·52
1951	Catch (*c*)	—	178·3	175·8	75·9	75·6	94·4
	Effort (*g*)	—	24·4	23·9	23·1	20·1	
	c/*g*	—	7·32	7·35	3·28	3·75	?
1952	Catch (*c*)	—	159·9	161·4	76·1	79·5	96·1
	Effort (*g*)	—	20·6	19·9	17·2	19·9	
	c/*g*	—	7·80	8·12	4·43	4·00	?
1953	Catch (*c*)	88·3	245·4	164·2	84·1	79·0	*
	Effort (*g*)	13·1	27·2	32·8	24·9	22·7	
	c/*g*	6·76	9·02	5·01	3·37	3·49	
1954	Catch (*c*)	160·2	266·9	190·0	109·5	107·2	55·1
	Effort (*g*)	21·6	42·1	41·7	37·1	36·7	11·7
	c/*g*	7·43	6·34	4·56	2·96	2·92	4·69
1955	Catch (*c*)	193·4	235·1	155·4	63·5	93·6	33·2
	Effort (*g*)	18·7	33·8	38·1	28·7	30·0	8·8
	c/*g*	10·32	6·96	4·08	2·22	3·12	3·78
1956	Catch (*c*)	100·6	343·3	196·4	90·1	95·6	67·1
	Effort (*g*)	22·2	56·2	72·3	64·4	54·0	14·6
	c/*g*	4·53	6·11	2·72	1·40	1·77	4·58
1957	Catch (*c*)	165·9	262·6	179·3	39·4	72·1	26·6
	Effort (*g*)	24·1	46·9	49·8	26·5	31·2	6·4
	c/*g*	6·90	5·60	3·60	1·49	2·31	4·14
1958	Catch (*c*)	249·0	391·8	221·3	87·4	54·9	32·1
	Effort (*g*)	31·6	71·6	60·2	40·0	39·5	9·7
	c/*g*	7·88	5·47	3·68	2·18	1·39	3·23
1959	Catch (*c*)	179·4	246·7	176·4	79·6	43·3	38·8
	Effort (*g*)	36·1	85·6	83·4	58·1	36·2	17·4
	c/*g*	5·00	2·88	2·12	1·37	1·20	2·22
1960	Catch (*c*)	307·7	246·4	124·3	76·0	37·9	23·3
	Effort (*g*)	97·6	81·8	79·4	65·2	45·0	17·9
	c/*g*	3·15	3·01	1·57	1·17	0·84	1·30
1961	Catch (*c*)	246·8	153·7	81·7	62·6	24·1	31·8
	Effort (*g*)	89·2	70·2	44·5	60·8	34·8	16·2
	c/*g*	2·77	2·20	1·84	1·03	0·70	2·00

* Records not available.

TABLE 3 (*Continued*)

Year	Statistic	March	April	May	June	July	August
1962	Catch (*c*)	235·4	149·0	56·5	20·3	19·6	8·1
	Effort (*g*)	67·5	58·4	39·9	25·6	27·6	8·7
	c/*g*	3·49	2·56	1·42	0·80	0·71	0·93
1963	Catch (*c*)	289·7	138·9	69·9	15·4	22·6	14·5
	Effort (*g*)	100·8	88·8	79·6	57·3	33·7	18·1
	c/*g*	2·88	1·56	0·88	0·27	0·67	0·80
1964	Catch (*c*)	154·4	233·3	108·7	16·7	32·7	*
	Effort (*g*)	41·5	67·7	56·1	27·2	32·0	
	c/*g*	3·72	3·45	1·94	0·61	1·02	

* Records not available.

are the inner areas of the Abrolhos island groups. The data from these inner areas are therefore best suited for estimates of crayfish population and recruitment levels.

The exponential decrease in the catch per pot-night (index of abundance) as the season (March–August) progresses, is the result of fishing mortality (F) and a factor M^1 which is the resultant of natural mortality, growth, and migration. If logarithms (to base e) of the catch per pot-night are plotted against time (corresponding months), the slope of the line provides an estimate of $F+M^1$. Both F and M^1 are instantaneous coefficients and when added equal a factor:

$$Z^1 = F+M^1. \qquad (1)$$

TABLE 4

TOTAL CATCH, EFFORT, AND CATCH PER UNIT EFFORT FROM OUTER GROUNDS AT THREE REGIONS OF THE ABROLHOS AREA

Catches (*c*) are given in thousands of pounds weight and effort (*g*) in thousands of pot-nights

Year	Pelsart Group			Easter Group			Wallabi and North I.		
	Catch (*c*)	Effort (*g*)	*c*/*g*	Catch (*c*)	Effort (*g*)	*c*/*g*	Catch (*c*)	Effort (*g*)	*c*/*g*
1955	253·4	51·4	4·9	185·2	22·2	8·3	221·9	30·0	7·4
1956	137·7	31·7	4·3	127·6	17·0	7·5	215·8	38·4	5·6
1957	314·9	62·8	5·0	279·0	44·6	6·3	462·2	80·3	5·8
1958	260·0	58·1	4·5	322·9	52·5	6·2	492·6	98·2	5·0
1959	463·7	104·3	4·5	418·5	82·5	5·1	799·3	191·9	4·2
1960	334·1	108·3	3·1	418·5	113·8	3·7	886·3	299·4	3·0
1961	403·3	159·4	2·5	532·7	159·2	3·3	1431·4	479·0	3·0
1962	655·3	302·3	2·2	512·5	188·1	2·7	1395·1	534·3	2·6
1963	429·3	217·1	2·0	477·9	238·0	2·0	970·7	560·8	1·7
1964	502·6	213·0	2·4	305·4	126·5	2·4	675·0	293·3	2·3

TABLE 5

TOTAL CATCH, EFFORT, AND CATCH PER UNIT EFFORT OF RED CRAYFISH EACH YEAR (JANUARY–APRIL) WITHIN STATISTICAL BLOCKS

Catches (c) are given in thousands of pounds weight and effort (g) in thousands of pot-nights

Year	Blocks 29 and 36			Block 38			Block 39			Block 44			Block 45		
	Catch (c)	Effort (g)	c/g	Catch (c)	Effort (g)	c/g	Catch (c)	Effort (g)	c/g	Catch (c)	Effort (g)	c/g	Catch (c)	Effort (g)	c/g
1948	489·7	86·1	5·7	*			*			*			*		
1949	*			1211·4	155·0	7·8	*			*			*		
1950	603·6	120·5	5·1	1789·7	290·3	6·2	*			*			*		
1951	1062·0	174·2	6·1	2418·2	330·0	7·3	*			*			*		
1952	1352·3	270·5	5·0	3211·9	468·7	6·9	*			8·9	7·1	1·3	140·8	84·8	1·7
1953	1423·3	368·1	3·9	2014·2	396·9	5·1	*			246·1	44·1	5·6	246·1	99·8	2·5
1954	1489·2	443·9	3·4	1905·3	404·1	4·7	919·7	191·4	4·8	30·0	17·1	1·8	234·9	140·6	1·6
1955	1273·4	362·7	3·5	2104·7	488·3	4·3	1298·1	236·2	5·4	47·3	20·7	2·3	292·8	144·0	2·0
1956	1731·7	484·8	3·6	1688·6	579·7	2·9	919·5	225·1	4·1	21·9	19·6	1·1	281·1	117·3	2·4
1957	1319·1	615·6	2·1	1169·4	560·7	2·1	1378·9	357·2	3·9	37·3	22·5	1·7	230·7	163·1	1·4
1958	1486·8	672·0	2·2	925·7	484·7	2·0	1339·6	500·2	2·7	615·3	122·1	5·0	266·1	204·3	1·3
1959	1829·6	870·4	2·1	1812·7	626·8	2·9	1674·2	529·2	3·2	996·4	244·6	4·1	*		
1960	2628·3	1603·2	1·6	1388·7	459·8	3·0	1653·4	555·0	3·0	1271·9	457·2	2·8	587·2	464·3	1·3
1961	2162·6	2130·3	1·0	730·1	439·8	1·7	1337·4	653·6	2·1	1624·8	584·5	2·8	497·9	413·7	1·2
1962	2529·4	1837·3	1·4	870·2	556·5	1·6	1132·1	772·9	1·5	1326·8	602·9	2·2	461·0	273·3	1·7
1963	3181·0	2266·7	1·4	779·2	693·5	1·1	1548·4	1077·0	1·4	2577·2	1592·6	1·6	842·9	775·8	1·1
1964	2241·1	1933·0	1·2	364·8	295·2	1·2	969·4	856·8	1·1	1916·7	1391·1	1·4	701·9	716·0	1·0

* Records not available.

TABLE 6

TOTAL CATCH, EFFORT, AND CATCH PER UNIT EFFORT OF WHITE CRAYFISH EACH SEASON (NOVEMBER–DECEMBER) WITHIN STATISTICAL BLOCKS

Catches (*c*) are given in thousands of pounds weight and effort (*g*) in thousands of pot-nights

Year	Blocks 29 and 36			Block 38			Block 39			Block 44			Block 45		
	Catch (*c*)	Effort (*g*)	*c*/*g*	Catch (*c*)	Effort (*g*)	*c*/*g*	Catch (*c*)	Effort (*g*)	*c*/*g*	Catch (*c*)	Effort (*g*)	*c*/*g*	Catch (*c*)	Effort (*g*)	*c*/*g*
1952	811·5	108·8	7·5	622·9	108·0	5·8	†	†	†	41·3	12·3	3·4	217·6	48·9	4·5
1953	809·6	155·1	5·2	606·5	89·1	6·8	†	†	†	46·7	10·1	4·6	228·7	66·3	3·4
1954	1142·8	153·9	7·4	923·2	157·5	5·9	296·1	50·4	5·9	83·4	17·4	4·8	283·7	72·2	3·9
1955	1230·7	196·0	6·3	735·6	195·0	3·8	76·7	14·6	5·3	184·9	29·0	6·4	441·2	79·8	5·5
1956	1041·5	228·9	4·6	808·3	264·6	3·1	268·4	47·3	5·7	53·5	24·1	2·2	639·8	146·2	4·4
1957	1256·4	263·3	4·8	714·4	182·3	3·9	904·5	189·0	4·8	375·5	43·3	8·3	870·1	177·6	4·9
1958	1155·6	352·8	3·3	585·3	195·6	3·0	791·9	199·2	4·0	284·3*	41·5*	6·9	121·2*	53·3*	2·3
1959	†	†	†	†	†	†	†	†	†	977·0	187·3	5·2	894·6	326·1	2·7
1960	1456·6	567·2	2·6	305·3	131·1	2·3	799·6	224·9	3·6	1476·5	353·2	4·2	603·7	238·5	2·5
1961	1701·6	705·2	2·4	398·5	143·5	2·8	1142·7	267·9	4·3	1665·8	286·7	5·8	1355·7	411·5	3·3
1962	1442·2	663·7	2·2	406·7	206·8	2·0	1234·0	388·6	3·2	2414·0	698·7	3·5	1114·1	401·6	2·8
1963	2007·9	545·6	3·7	239·0	58·8	4·1	1405·6	279·2	5·0	2922·4	659·8	4·4	1049·4	307·4	3·4

* Incomplete totals. † Records not available.

The fishing mortality is generated by the sum of the units of effort and related to the effective total effort (f) by a factor q, the catchability coefficient (Holt 1960), in the form:

$$F = qf. \tag{2}$$

Equation (1) may then be written:

$$Z^1 = M^1 + qf, \tag{3}$$

which is a standard linear equation with variables Z^1 and f. The symbol f signifies that the total effective effort is known. However, when using gross commercial statistics the true effective effort is not known and therefore the symbol g is used denoting the total recorded effort for the period of time under discussion. The symbol g then replaces f in equations (2) and (3).

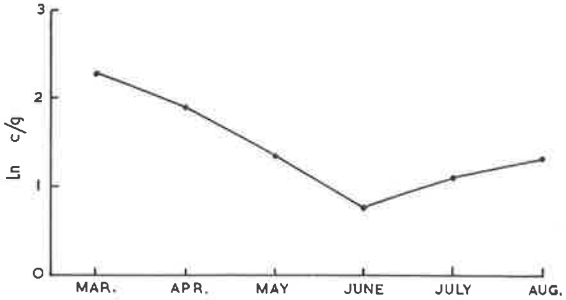

Fig. 3.—Logarithms (to base e) of monthly catches per pot-night (c/g) at the Wallabi (including North I.) Group, Inner Area, Abrolhos, 1955.

The best estimates of Z^1 will be obtained if g is constant throughout the season. Since in practice g varies, a source of error is introduced into the analysis. However, the decline in the indices of abundance is sufficiently steady to permit the use of the seasonal estimates of Z^1 to show trends in the population and recruitment levels. Certainly, during the first 3 months of a normal season the catch per pot-night falls steadily as shown in Figure 3. In June the index of abundance appears to be lower than the actual abundance because some adult crayfish are moulting and are not vulnerable as they do not feed immediately before and after moulting. This is balanced in July when there is an increase in the index because the newly moulted crayfish, slightly increased in size, are now commencing to feed. The catch per unit effort rises further in August because the newly moulted crayfish are feeding, and also because of recruitment by growth and migration. However, since the season closes on August 15, and the effort expended (and therefore F) during this month is very small (approximately 5%), the total mortality coefficient (Z^1) has been calculated over the period from March to July, and the slight increase in abundance during August has been incorporated in the off-season recruitment.

By calculating the line of best fit for plots of Z^1 against g for a number of years (i.e. equation (3)) estimates are obtained for the average values of M^1 and q during those years. The intercept of the regression line on the y axis (i.e. no fishing effort) is the estimate of $\bar{M}^1$, while the slope of the line is q (catchability coefficient).

Having obtained values for Z^1 in each season, and values for $\bar{M}^1$ and q, the fishing mortality (F) can be calculated either from equation (1), which assumes natural mortality, migration, and growth components to be constant from one year to another, or from equation (2), which is more realistic since M^1 is likely to fluctuate annually. The calculation of F from the multiple qg has been applied except where there has been evidence of a change in the value of q.

For the years in which monthly records of pots fished were not available (i.e. before 1950), the total effort in terms of pot-nights has been calculated from the average number of men operating and an estimate of the average number of pots per man. Since Z^1 could not be calculated directly for these years, the catchability coefficient (q), calculated from the years in which monthly pot data were available, was multiplied by the seasonal effort to give estimates of F (equation (2)).

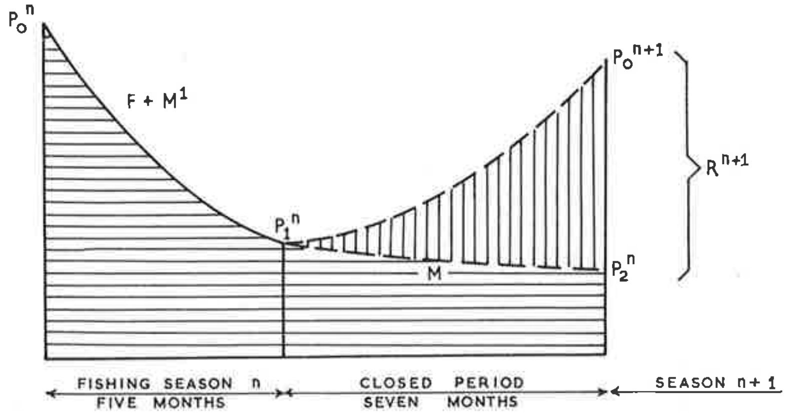

Fig. 4.—Diagram showing the fall in crayfish abundance from the beginning of the season P_o^n to the end of the fishing season P_1^n and to the end of the closed period P_2^n. The abundance of crayfish at the beginning of the next season is given by P_o^{n+1}.

These estimates of F then provide information on the average population levels ($\bar{P}$) for each season from:

$$C = PF \tag{4}$$

where C = the catch for a season.

Catchable stock at the beginning of the season (P_o) and at the close of the season (P_1) can then be calculated from:

$$\cancel{P_o = Z^1/\bar{P}\{1 - \exp(-Z^1)\}}, \quad P_0 = z'\bar{P}/1 - e^{-z'} \tag{5}$$

and

$$P_1 = P_o \exp(-Z^1). \tag{6}$$

The level to which P_1 would have fallen by the beginning of the following season (P_2), if there had been no recruitment, can also be calculated from:

$$P_2 = P_1 \exp(-7M/5), \tag{7}$$

where M = natural mortality for the 5-month fishing season.

During the period closed to fishing (7 months), natural mortality may not be at the same rate as M^1, but tests using various values for M for the closed period showed that the precise value makes little difference when F is high.

Although the catchable stock present at the beginning of year n (P_0^n) would have fallen to P_2^n by the end of that year, the catchable stock at the beginning of the following year ($n+1$) has recovered to the level of $P_0^{(n+1)}$. The replenishment which took place during the closed period is then:

$$R^{(n+1)} = P_0^{(n+1)} - P_2^n \tag{8}$$

Figure 4 illustrates this model showing the various levels of the population during a year. The replenishment during the 7 months when the areas are closed to fishing may result from (1) growth of the undersize crayfish already present on the grounds; (2) migration from waters outside the fishing areas; or (3) a combination of (1) and (2).

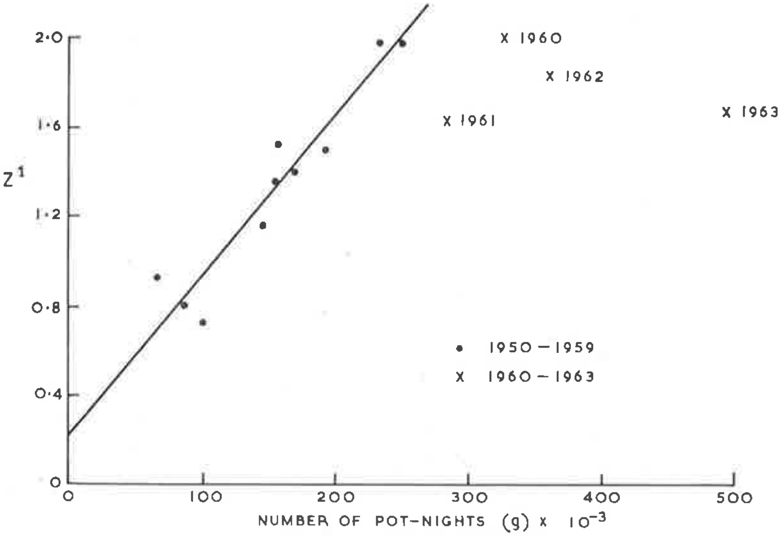

Fig. 5.—Relation between total mortality (Z^1) and effort (g) for Easter Group, Inner Area, Abrolhos, 1950–59.

The exploitation rate (E) is obtained from the ratio of the catch in a particular season (C) to the catchable stock present at the commencement of that season (P_0), since

$$C = EP_0 \tag{9}$$

(*b*) *Parameters Estimated for Inner Areas*

Tables 7, 8, and 9 show the values derived by the method outlined above, for the inner areas of the Easter, Pelsart, and Wallabi (including North I.) groups of the Abrolhos, respectively. In each set of data the values of Z^1 generally increase with g.

(i) *Easter Group*

Figure 5 shows that the relation between total mortality (Z^1) and effort (g) was linear from 1950 to 1959, but from 1960 to 1963 fishing effort increased without a

TABLE 7

EASTER GROUP (INNER AREA), ABROLHOS

Commercial catches (c), mean population March–July ($\bar{P}$), initial population at opening of season (P_0), population at close of season (P_1), population at end of year, assuming no growth or migration (P_2), and recruitment (R) are given in thousands of pounds weight. Effort (g) is given in thousands of pot-nights. Other statistics are: Z^1, total mortality coefficient; F, fishing mortality coefficient; and E, exploitation rate

Year	Catch March–July (c)	Effort March–July (g)	c/g	Z^1	F*	$\bar{P}$	P_0	P_1	P_2	R	E (%)
1943	145·8	(9·2)	(15·8)		(0·066)	(2209)	(2544)	(1907)	(1398)		6
1944	147·4	(9·2)	(16·0)		(0·066)	(2233)	(2571)	(1928)	(1413)	(1173)	6
1945	141·8	(9·8)	(14·5)		(0·070)	(2026)	(2336)	(1745)	(1279)	(923)	6
1946	229·9	(14·7)	(15·6)		(0·105)	(2190)	(2568)	(1852)	(1358)	(1289)	9
1947	428·1	(31·2)	(13·7)		(0·222)	(1928)	(2388)	(1532)	(1123)	(1030)	18
1948	448·5	(36·7)	(12·2)		(0·262)	(1712)	(2160)	(1331)	(976)	(1037)	21
1949	566·9	(62·3)	(9·1)		(0·444)	(1277)	(1749)	(899)	(659)	(773)	32
1950	603·8	87·3	6·9	0·800	0·622	971	1410	633	493	751	43
1951	475·3	67·9	7·0	0·919	0·484	982	1498	596	324	1005	32
1952	497·6	98·7	5·0	0·720	0·704	707	992	483	473	668	50
1953	613·7	148·0	4·2	1·156	1·055	582	980	307	267	507	63
1954	780·0	157·7	4·9	1·364	1·124	694	1275	328	234	1008	61
1955	579·9	170·0	3·4	1·404	1·212	478	891	220	168	657	65
1956	629·5	158·0	4·0	1·526	1·127	559	1088	235	134	920	58
1957	744·9	193·4	3·9	1·508	1·379	540	1045	231	193	911	71
1958	793·3	231·8	3·4	1·976	1·653	480	1098	152	97	905	72
1959	687·3	249·1	2·8	1·984	1·776	387	891	123	92	794	77
1960	724·6	328·9	2·2	2·005	1·783	406	941	127	93	849	77
1961	622·9	284·5	2·2	1·635	1·413	441	896	175	128	803	70
1962	699·8	360·5	1·9	1·830	1·608	435	949	152	111	821	74
1963	622·9	496·3	1·3	1·680	1·458	427	882	164	120	771	71
1964	538·4	294·8	1·8	2·039	1·817	296	694	90	66	574	78

* From 1943–61, $q = 7\cdot13\times10^{-6}$ used to get F, ($F = qg$); from 1962–64, $\bar{M}^1 = 0\cdot222$ used to get F, ($F = Z^1-\bar{M}^1$).

TABLE 8

PELSART GROUP (INNER AREA), ABROLHOS

Commercial catches (c), mean population March–July ($\bar{P}$), initial population at opening of season (P_0), population at close of season (P_1), population at end of year, assuming no growth or migration (P_2), and recruitment (R) are given in thousands of pounds weight. Effort (g) is given in thousands of pot-nights. Other statistics are: Z^1, total mortality coefficient; F, fishing mortality coefficient; and E, exploitation rate

Year	Catch March–July (c)	Effort March–July (g)	c/g	Z^1	F*	$\bar{P}$	P_0	P_1	P_2	R	E (%)
1943	20·9	(4·4)	(4·8)		(0·034)	(615)	(879)	(409)	(147)		
1944	36·6	(7·3)	(5·0)		(0·056)	(654)	(946)	(432)	(156)	(799)	(4)
1945	35·1	(6·1)	(5·8)		(0·047)	(747)	(1074)	(493)	(177)	(918)	(3)
1946	43·7	(7·9)	(5·5)		(0·061)	(716)	(1037)	(470)	(169)	(860)	(4)
1947	100·2	(12·9)	(7·8)		(0·099)	(1012)	(1489)	(649)	(234)	(1320)	(7)
1948	314·9	(35·2)	(8·9)		(0·270)	(1166)	(1847)	(680)	(245)	(1613)	(17)
1949	620·6	(56·9)	(10·4)		(0·458)	(1355)	(2318)	(707)	(255)	(2073)	(27)
1950	671·6	96·3	7·0	1·076	0·740	908	1480	503	314	1225	45
1951	451·9	90·2	5·0	1·346	0·693	652	1188	310	124	874	38
1952	350·9	76·9	4·6	0·984	0·591	594	933	349	201	809	38
1953	283·3	68·3	4·2	1·629	0·525	540	1095	215	46	894	26
1954	397·1	69·1	5·8	1·121	0·531	748	1245	406	178	1199	32
1955	407·7	114·0	3·6	1·638	0·876	465	945	183	63	767	43
1956	390·8	125·6	3·1	1·953	0·965	405	922	131	33	859	42
1957	333·7	99·8	3·3	1·238	0·766	436	761	221	114	728	44
1958	287·0	83·0	3·5	1·332	0·637	451	817	216	82	703	35
1959	275·8	87·3	3·2	1·791	0·670	412	886	148	31	804	31
1960	314·9	122·1	2·6	1·320	0·938	336	606	162	95	575	52
1961	339·5	104·7	3·2	2·070	0·804	422	1000	126	21	905	34
1962	364·7	154·4	2·4	1·960	1·229	297	677	95	34	656	54
1963	348·0	192·4	1·8	1·945	1·214	287	651	93	33	617	53
1964	253·1	103·3	2·5	2·400	1·669	152	400	36	13	367	63

* From 1943–61, $q = 7\cdot68\times10^{-6}$ used to get F, ($F = qg$); from 1962–64, $\bar{M}^1 = 0\cdot731$ used to get F, ($F = Z^1 - \bar{M}^1$).

TABLE 9

WALLABI GROUP AND NORTH I. (INNER AREAS), ABROLHOS

Commercial catches (c), mean population March–July ($\bar{P}$), initial population at opening of season (P_o), population at close of season (P_1), population at end of year, assuming no growth or migration (P_2), and recruitment (R) are given in thousands of pounds weight. Effort (g) is given in thousands of pot-nights. Other statistics are: Z^1, total mortality coefficient; F, fishing mortality coefficient; and E, exploitation rate

Year	Catch March–July (c)	Effort March–July (g)	c/g	Z^1	F*	$\bar{P}$	P_o	P_1	P_2	R	E (%)
1943	40·3	(2·6)	(15·5)		(0·011)	(3664)	(5304)	(2402)	(805)		1
1944	117·8	(8·9)	(13·2)		(0·036)	(3272)	(4789)	(2116)	(709)	(3984)	3
1945	89·8	(11·5)	(7·8)		(0·047)	(1911)	(2810)	(1228)	(411)	(2101)	3
1946	242·6	(30·8)	(7·9)		(0·125)	(1941)	(2951)	(1192)	(399)	(2540)	8
1947	396·7	(29·4)	(13·5)		(0·120)	(3306)	(5016)	(2037)	(682)	(4617)	8
1948	296·8	(34·7)	(8·6)		(0·141)	(2105)	(3222)	(1281)	(429)	(2540)	9
1949	499·7	(53·9)	(9·3)		(0·219)	(2282)	(3610)	(1328)	(445)	(3181)	14
1950	498·4	93·2	5·4	0·984	0·379	1315	2064	770	330	1619	24
1951	505·6	91·6	5·5	1·124	0·373	1355	2256	733	257	1926	22
1952	477·0	77·5	6·1	1·037	0·315	1514	2434	864	314	2177	20
1953	661·0	120·7	5·5	1·192	0·491	1346	2305	701	263	1991	29
1954	833·6	179·1	4·7	1·305	0·729	1143	2047	555	248	1784	41
1955	741·1	149·3	5·0	1·719	0·608	1219	2552	457	96	2304	29
1956	826·1	269·0	3·1	1·715	1·095	754	1577	284	119	1481	52
1957	719·3	178·5	4·0	1·737	0·726	991	2089	368	89	1970	34
1958	1004·4	243·0	4·1	2·178	0·989	1016	2495	282	53	2406	40
1959	725·5	299·3	2·4	1·746	1·218	596	1260	219	105	1207	58
1960	792·3	368·9	2·2	1·795	1·014	781	1681	279	93	1576	47
1961	567·8	299·5	1·9	1·760	0·979	580	1233	212	71	1140	46
1962	480·8	219·1	2·2	2·175	1·394	345	847	96	32	776	57
1963	536·5	360·2	1·5	2·335	1·554	345	892	86	29	860	60
1964	545·7	224·6	2·4	2·155	1·374	397	968	112	38	939	56

* From 1943–59, $q = 4\cdot07\times10^{-6}$ used to get F, ($F = qg$); from 1960–64, $\bar{M}^1 = 0\cdot781$ used to get F, ($F = Z^1 - \bar{M}^1$).

corresponding rise in total mortality. In recent years the effect of the increasing number of pots fished has been to cause a decline in catchability (q) rather than an increase in total mortality. For the period from 1950 to 1959, the regression of total mortality on effort was:

$$Z^1 = 7 \cdot 13 \times 10^{-6} g + 0 \cdot 222.$$

Therefore,

$$M^1 = 0 \cdot 222 \text{ (s.d. } 0 \cdot 13\text{) and } q = 7 \cdot 13 \times 10^{-6}.$$

Estimates of q in recent years, obtained from $F = qg$, were:

$$1960 = 5 \cdot 42 \times 10^{-6};\ 1961 = 4 \cdot 98 \times 10^{-6};$$
$$1962 = 4 \cdot 46 \times 10^{-6};\ 1963 = 2 \cdot 94 \times 10^{-6}.$$

Before the fishing season of 1964, the effort was restricted by limiting the number of pots to three per registered foot length of boat with a maximum of 200 pots per boat. This reduction in the number of pots fishing during 1964 had the immediate effect of increasing the catchability (q) to $6 \cdot 16 \times 10^{-6}$, restoring it almost to the level of 1950–59.

(ii) *Pelsart Group*

Although total mortality (Z^1) generally increased with fishing effort (g), this relation was not as clear at the Pelsart (Table 8) as at the Easter Group (Table 7). The regression of total mortality on effort for the years 1950–1961 at the Pelsart Group was:

$$Z^1 = 7 \cdot 68 \times 10^{-6} g + 0 \cdot 731,$$

so that

$$M^1 = 0 \cdot 731 \text{ (s.d. } 0 \cdot 5\text{) and } q = 7 \cdot 68 \times 10^{-6}.$$

In 1963 the fishing effort increased without a corresponding rise in total mortality, indicating a decline in catchability (q) similar to that shown at the Easter Group.

(iii) *Wallabi Group and North I.* (Table 9)

The line of best fit for the regression of Z^1 on g calculated for the period from 1950 to 1959 was:

$$Z^1 = 4 \cdot 07 \times 10^{-6} g + 0 \cdot 781.$$

Therefore,

$$M^1 = 0 \cdot 781 \text{ (s.d. } = 0 \cdot 20\text{) and } q = 4 \cdot 07 \times 10^{-6}.$$

The reason for the lower value of q for this area compared with corresponding values for the Easter and Pelsart groups is not apparent; possibly there was a slight difference in fishing practice from one area to another. The estimate of catchability at the Wallabi (including North I.) Group dropped to $2 \cdot 75 \times 10^{-6}$ in 1960 when the fishing effort reached a maximum (Table 9). In 1964, when the effort was reduced, the estimate of catchability rose to $6 \cdot 12 \times 10^{-6}$, similar to the values for the Easter and Pelsart groups up to 1960.

Tables 7–9 show that in 1964 total mortality (Z^1) was relatively high at each locality in spite of the decrease in effort. One contributing factor to this may have been poorer recruitment during the 1964 season owing to heavy pre-recruit mortality during the previous season when fishing effort was particularly high. Another factor may have been the adverse weather in the latter portion of the 1964 season which may have lessened the effective effort at that time, because pots were pulled less frequently. Since the effort may then have been overestimated, the catch per unit effort would have been less during the latter part of the season, and the total mortality (Z^1) would have to be set at a higher value. The more detailed records collected since 1964 will enable the influence of weather conditions to be eliminated from future estimates of abundance (catch per unit effort).

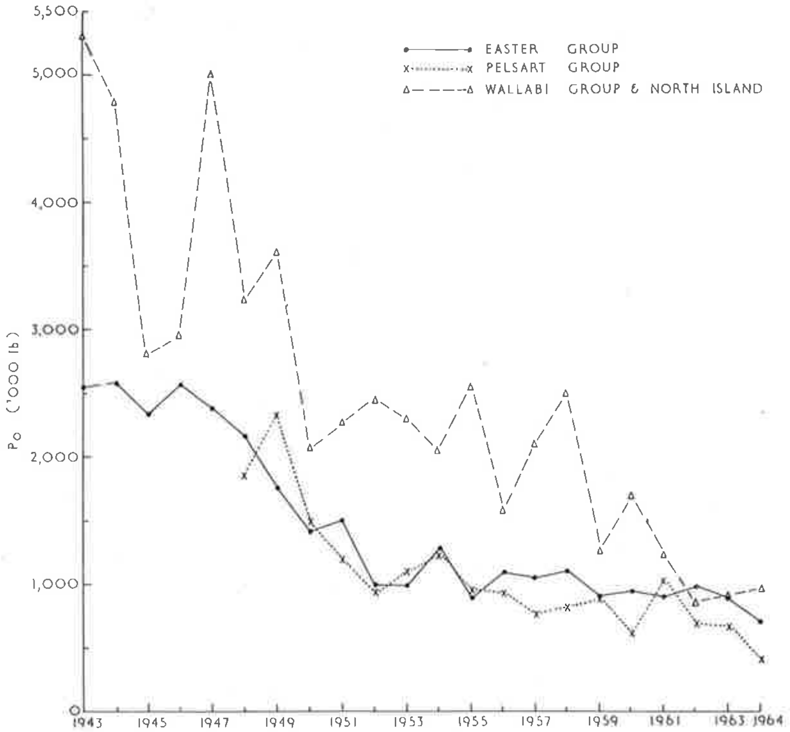

Fig. 6.—Population at beginning of each season (P_0), Inner Areas, Abrolhos.

(c) *Population and Recruitment Levels*

(i) *Easter Group*

Figure 6 shows that the population level at the commencement of each season (P_0), initially fairly stable, fell rapidly between 1948 and 1952 and thereafter showed only a slight downward trend. In recent years (1959–63) the population level appeared to have stabilized, but at the opening of the fishing season in 1964 the population level was lower than at the corresponding time in any previous year.

Figure 7 shows that over the past 20 yr there has been a relatively slight downward trend in recruitment (R) which appeared to have stabilized in recent years but fell again from 1963 to 1964.

Table 7 shows that the exploitation rate (E) increased with effort (g) until 1957 and then remained steady although the fishing effort increased by more than 100%. Although the effort expended within the Easter Group in 1964 was only 59% of that in 1963, the exploitation rate remained at the same high level.

(ii) *Pelsart Group*

The results of the calculations summarized in Table 8 show an apparent increase in the population level in the early years of the fishery (1943–49), but the estimates for this period are likely to be inaccurate. Since the fishermen at the Pelsart Group are known to have been less dependent on crayfish than upon other fish during the early years, their catches of crayfish were much lower than at the other island groups. However, as the effort has been recorded on the assumption that pots were pulled daily, the estimated effort is too high in these years. This has resulted in estimates of population level which are too low.

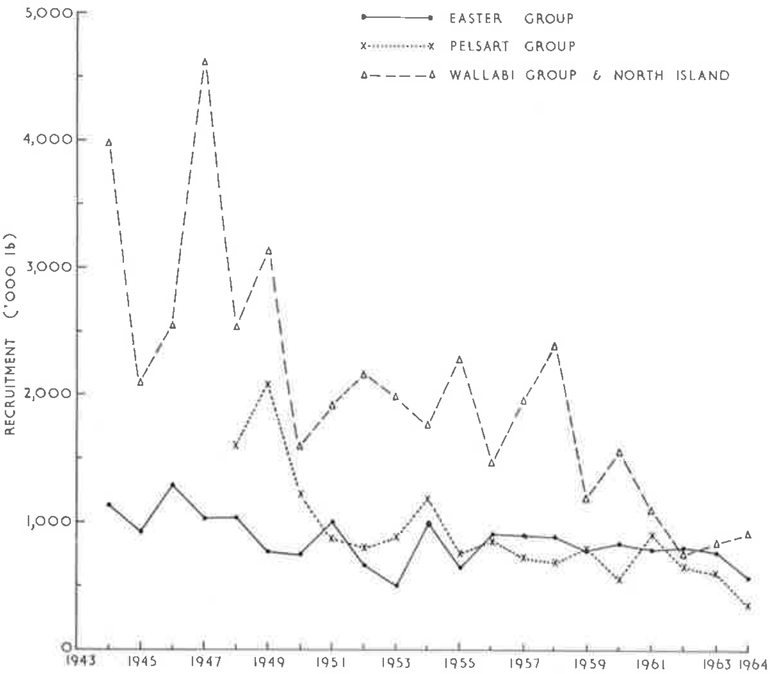

Fig. 7.—Annual recruitment, Inner Areas, Abrolhos.

Since 1948, when the estimates of fishing effort expended each year at Pelsart Group are more realistic, the estimate of population size (P_0) has followed a similar downward trend to that of the Easter Group (Fig. 6), the population reaching its lowest level in 1964. Recruitment, initially high at the Pelsart Group, is now lower than at the Easter Group as shown in Figure 7. Exploitation rate did not rise at high levels of effort (Table 8). Although the fishing effort within the Pelsart Group decreased by 46% from 1963 to 1964 the exploitation rate was higher in 1964 than in any previous season. This again indicates that much of the high level of effort expended in recent seasons has been ineffective.

(iii) *Wallabi Group and North I.*

Figure 6 indicates that the population present at the commencement of each season (P_0) was at a high level from 1943 to 1949, fluctuated about a lower level from 1950 to 1958, and has since declined to a relatively low level which has been maintained since 1962. Figure 7 shows a similar decline in recruitment.

Exploitation rate (E) generally increased with effort, except at the particularly high levels of effort in 1960 and 1963 (Table 9). In 1964 the fishing effort in this area was reduced to 62% of that expended in 1963, but the exploitation rate remained substantially the same.

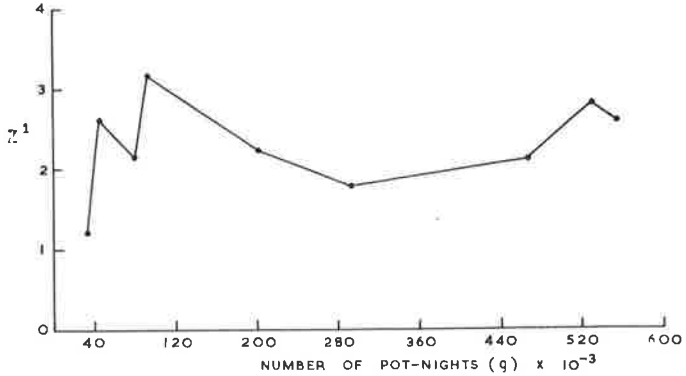

Fig. 8.—Relation between mortality (Z^1) and effort (g), Wallabi (including North I.) Group, Outer Area, Abrolhos, 1955–63.

IV. ABROLHOS, OUTER AREAS

For the analysis of data from the inner areas, the assumption had to be made that the density of crayfish was relatively uniform and also that the effort was spread over the grounds throughout the season. However, in the outer areas these conditions certainly did not apply. Early in the season the weather conditions permit the fishermen to work west of the island groups in exposed areas which cannot be worked in June and July. Also, fishermen are able to move their gear greater distances than those men confined to the inner areas. As a result the rate of decrease in the catch per unit of effort during a season has very little correlation with the fishing effort expended.

Attempts were made to derive the total mortality coefficient for each season from the slope of the regression of the logarithm of the catch per unit of effort for each month against time, but the resultant values for Z^1 were very high and had no relation to the effort expended, as shown in Figure 8. Consequently estimates of M^1, F, and q could not be determined. However, as the fishermen tend to follow a similar routine each year the trends in the annual catch per unit of effort can be followed from the commencement of the fishery and compared with the inner areas. The catch per unit of effort has been calculated for the outer areas using the total catch and total number of pot-nights for each season (Table 4).

Table 4 shows that since fishing commenced on the outer grounds (in 1955) the seasonal catch per pot-night has decreased considerably in each area. This decline in the average catch per unit of effort reflects the drop in abundance on the grounds. One fisherman who fishes in the outer area of the Pelsart Group remarked recently that when he first fished the outside waters it was profitable to move his crayfish pots across a reef area and then to re-pot the same reef. However, the abundance has now been reduced to a point which makes it no longer profitable to pot a reef a second time during the first few weeks of the season.

The level of abundance on the outer reefs at the Pelsart Group was constant during the period from 1955 to 1958 when the effort was low. The effort increased sharply from 1959 and the fishing mortality generated by this effort has apparently been sufficient to reduce the average abundance year by year.

At the Easter Group (Table 4) the density of crayfish on the outer reefs appears to have been higher initially than on the reefs outside the Pelsart Group. Yet, with the expenditure of relatively little effort, the density around the Easter Group declined. This could be interpreted as the result of a smaller area of outer reefs around the Easter Group than around the Pelsart Group.

The density of crayfish on the outer reefs of Wallabi and North I. is now much the same as around the other island groups, but the area fished is apparently greater than either the Pelsart or Easter groups.

V. Coastal Fishery

(*a*) *The Red Crayfishery*

The "red" crayfish taken on the mainland coast from January to August are of size and colour range similar to those at the Abrolhos area. The fishery is concentrated mainly in the waters south of Geraldton because most of the Geraldton fishermen cease fishing the coastal areas at the end of January to prepare for the Abrolhos fishery. Although the season does not close until August 15, inclement weather prevents many of the fishermen from operating after April or May. In 1963 for example, the catch during the period January to April represented 95% of the red crayfish production. Therefore, the catch and effort data for this period have been selected for analysis.

Although for each area (block) along the coast, the catch and effort data are recorded for each month, the variation in average catch per unit effort from one month to another does not necessarily reflect changes in abundance in this instance. During January and February many of the crayfish entering pots have eggs attached to the pleopods and, by law, have to be returned to the sea. However, January is regarded as the month of maximum larval release and shortly after most of the mature females undergo a moult. As many crayfish are, therefore, either not vulnerable to the crayfish pot or must be returned to the sea, the catch per unit of effort is depressed during January and February. Consequently, estimates of mortality could not be made from the data for the coastal fishery because the catch per unit effort did not fall from month to month as a result of fishing (Fig. 9). However, the average catches per unit of effort for the 4-month period have been calculated (Table 5) and do give indices of abundance within each block from year to year.

Table 5 shows that, with the exception of block 45, the catches per pot-night for the coastal areas have decreased in a manner similar to the outer areas of the Abrolhos. In block 45 the indices of abundance have been uniformly low. This may reflect a low level of abundance. However, it may be due to the fact that Geraldton fishermen may have worked their gear spasmodically during February and March of each year while preparing for the season at the Abrolhos area. This would cause the effort figure to be greatly overestimated and the indices of abundance to be low. The indices are also low in block 44 during the years of low effort but in 1958, when the intensive fishing commenced, the index was comparable with the southern areas.

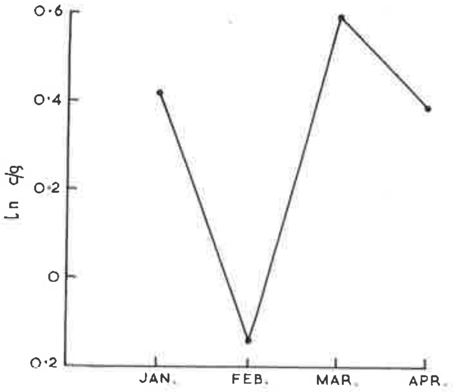

Fig. 9.—Logarithms (to base e) of monthly catches per pot-night (*c*/*g*) in block 39, 1963.

The general trend in the indices indicates that the state of the coastal fishery is very similar to the Abrolhos fishery; that is to say, the abundance is declining and the exploitation rate is high.

(*b*) *The White Crayfishery*

As shown by George (1958), the pale-coloured "white" crayfish represent a recently moulted immature phase. Soon after moulting these white crayfish are captured as they move away from coastal reefs. Differences in behaviour enable them to be fished to the exclusion of red crayfish at that time. Although the season opens on November 15, white crayfish are seldom ready to feed then, and are not vulnerable to the fishing gear until the last week of the month. Production reaches a peak during the first and second weeks of December and then falls away during the last week. It has been estimated that the fishermen operate for about 30 days on the white crayfish and this value has been used to transform the total number of pots into pot-nights, assuming as before, that pots are pulled daily. The trends of the annual indices of abundance (*c*/*g*) in each block for recent years are shown in Table 6.

The white crayfish production represents approximately 33% of the annual catch of *P. cygnus* and therefore is of considerable economic importance. The catch of white crayfish is also of biological importance because the majority of these had attained legal size only a few weeks before (at the last moult) and so were being subject to exploitation for the first time. Consequently the white crayfish afford some measure of recruitment.

Figure 10 shows the average catch of white crayfish per pot-night for each year, the coastal data being separated into areas south and north of 30°S. The values obtained before 1947 cannot be used as indices of abundance, mainly because the effort has been over-estimated by the assumption that all the pots used were fished every day of the season, and also because the number of pots per man had to be estimated by extrapolation.

South of 30°S., the abundance of white crayfish has declined considerably since 1949. In 1963 the catch per pot-night rose to the level of 1959. This could reflect improved recruitment during 1963 compared with that in the years 1960–62. However, there were changes in the statistics because of pot restrictions introduced before the white crayfish season of 1963. Limitation of the number of pots per foot of boat has had two effects. Firstly, because some fishermen used about 10% more pots than recorded in their statistical returns, the catch per unit of effort was slightly over-estimated. Secondly, the reduction in the number of pots has probably restored the catchability coefficient (q) which was depressed from 1960 to 1962 as the density of pots increased.

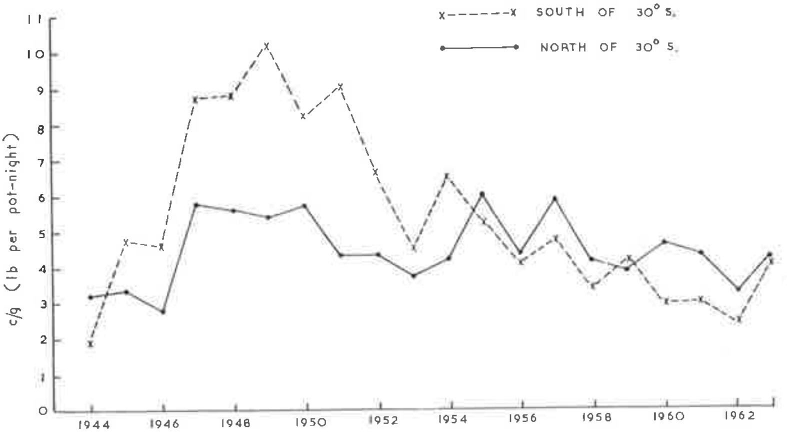

Fig. 10.—Annual catch per pot-night (c/g) for the white crayfishery north and south of 30°S.

The general impression of the 1963 season gained from information supplied by fishermen, is that the actual abundance of crayfish had not increased but that the higher index was due to a slight increase in the catchability coefficient of the pot and to fishermen using more pots than the number recorded on their returns. The abundance of white crayfish, therefore, has not fallen to the extent indicated by the values for 1960–62 in Figure 10 although there has been a downward trend.

The trends for each block (Table 6) follow closely the trend for the whole area. However, the indices of abundance for the Jurien Bay area (block 39) are higher than the other areas for the same years.

North of 30°S., the indices of abundance (Fig. 10) were relatively high during the years 1947–50, although not as high as those for south of 30°S. From 1951 to 1963 the level has fluctuated with little suggestion of a downward trend. However, an examination of the two main blocks (44 and 45 in Table 6) shows that one area has tended to bias the indices in the other. Before about 1955, block 45 produced more than 90% of the crayfish taken north of 30°S. (Sheard 1962, table 6). It seems highly likely, therefore, that before 1955 block 45 produced about 90% of the white crayfish. Therefore, the indices of abundance for the years 1944–51 in Figure 10 can be regarded as the indices for block 45. Thus the indices of abundance were 5·4–5·8 within the period from 1947 to 1950 and have declined in recent years (Table 5) in a similar trend to that in the southern areas.

Block 44 has been intensively fished only during the last 8 yr. During this time the indices of abundance have fallen from approximately 8 lb per pot-night to 4 lb per pot-night.

VI. Discussion

(*a*) *Abrolhos Area*

The crayfish stocks in the inner areas of the Abrolhos each reacted to fishing pressure in a similar manner. The population level at the commencement of each season was high in the early years of the fishery but gradually fell as the effort increased each year. Exploitation rates rose to high levels and then remained steady over the past few years, in spite of further increase in effort. The high levels of effort depressed catchability rather than increased fishing mortality. Regulations which were introduced towards the end of 1963 and which limit the number of boats and the number of pots per boat, have reduced the recorded effort to some extent, and restored the value of q without lessening the effective effort.

The high exploitation rate in recent years has decreased the abundance of crayfish remaining on the grounds at the end of each season to a very low level. As a consequence, the major portion of the population available at the commencement of each season must result from replenishment of the fishing grounds during the preceding closed period. However, this has declined steadily as the fishing effort has increased.

There are two sources of replenishment:

(1) By movement of crayfish of all sizes from adjacent areas (including the outer grounds); and

(2) By growth of undersize crayfish present on the inner grounds into legal-size fish.

Since information upon the movement of crayfish into the inner areas is not available it is not possible to measure the extent to which these areas are dependent upon the outer grounds. However, the extent of any such replenishment from the outer grounds must have been reduced in recent years because of the development of the fishery on these grounds since 1955.

There is a high density of undersize crayfish in the inner areas and the growth of these during the closed period must contribute greatly to the availability of legal size crayfish. The selectivity of the crayfish pots being used is such that very large numbers of undersize crayfish are caught by the fishermen each day. One of the authors (B.K.B.) has seen as many as 40 undersize crayfish caught in one pot. Many of these juveniles may not survive when returned to the sea. McKay (personal communication) has observed Abrolhos groper (*Choerodon cyanodus* (Richardson)) taking crayfish thrown overboard from a fishing boat operating in the inner area of the Easter Group. Such fishing mortality would increase with the number of pots in use. Fish traps were also operated at the Abrolhos area until 1964 and undersize crayfish were further depleted by their illegal use as bait for these traps.

The fall in the catch per unit of effort for the outer areas of the Abrolhos closely follows the reduction in this statistic for the inner areas. This indicates that the fishing pressure in the outer areas is reducing the population level during each season to the same level of abundance as that in the inner areas, i.e. that the exploitation rate is at a similar high level. If this is true, each island group of the Abrolhos area can be regarded as an integral area which is being heavily fished and which is largely dependent upon replenishment by growth for each season's fishery. In the outer grounds some new reefs with high initial yields will no doubt be discovered occasionally, but the few which have been discovered in recent years have not maintained high production rates, indicating that density of crayfish and rate of recruitment to these deeper reefs are both relatively low.

(*b*) *Coastal Fishery*

Sheard (1962) gives a general description of the development of the coastal fishery. Before 1954 very little fishing was carried out in the area between Dongara and Cervantes. Since then the Fremantle boats have gradually explored and opened up the shallow and deep-water areas between Cervantes and Beagle I. In recent years Geraldton and Dongara fishermen have moved south of Dongara with the result that all the grounds between Fremantle and Geraldton are now being worked.

The pattern of development has enabled high catch rates to be maintained by those fishermen who have explored the new grounds, and the total production to rise steadily. However, as the area of exploitation has increased the total accumulated stock has been reduced in both the fished and unfished areas. A reduction of density in the unfished areas would occur as crayfish from these areas intermingled with those in the exploited areas during periods of random wandering.

A reduction in the accumulated stock has been manifest by a decrease in the catch per unit of effort which is now at a level similar to that for the Abrolhos area. The fishery has passed through the developmental phase and may now be regarded as being fully exploited with very few new areas of high productivity likely to be found. The exploitation rate is probably very high and the fishery is now largely dependent upon the level of recruitment into the legal size fraction of the population during the preceding close season. The principal source of replenishment for the coastal fishery is the undersize crayfish present in large numbers along the shallow-water (up to 15 fm) coastal reefs. Inaccessible areas provide some replenishment but the fraction from this source must be small as the catch per unit effort is now very low on all fishing grounds.

Estimates of recruitment cannot be obtained from the statistical data for the coastal red fishery. However, the statistics from the white crayfishery can be used to study trends in the level of recruitment. The modal length of the white crayfish stock is close to the legal minimum length (3-in. carapace), and current studies of growth rate have shown that this length is attained during the closed period immediately before their capture. Since this is the first time that the juvenile crayfish have been fully exposed to commercial exploitation, the relative abundance of white crayfish may be regarded as an index of the level of recruitment for that season.

In each statistical block the catch per pot-night has steadily declined (Table 6) thereby indicating a fall in the number of crayfish reaching legal size. Although the introduction of pot restrictions before the 1963 season resulted in an increase in the recorded catch per unit of effort, this does not necessarily indicate a real increase in abundance during that year. White crayfish are caught over a restricted area compared with the red crayfish grounds and the reduced effort in 1963 has apparently caused an improvement in the catchability coefficient of the craypot similar to that demonstrated at the inner areas of the Abrolhos area in 1964. Also, there are indications that some fishermen used a greater number of pots than were recorded on their statistical returns. These two factors would increase the catch per unit of recorded effort without an increase in abundance.

The general reduction in the abundance of white crayfish strongly indicates a decline in the annual level of recruitment. One explanation might be that the mature stock remaining is insufficient to maintain the level of recruitment. Direct evidence on this point is not yet available. However, discussions with fishermen indicate that the number of undersize crayfish caught per pot at the beginning of each season has not changed appreciably. The more obvious cause of the decline in recruitment is an increasing mortality amongst undersize crayfish as the fishing effort has increased. This aspect has already been discussed with reference to the decline in recruitment at the Abrolhos area.

(*c*) *Total Population*

The evidence from each of the areas at the Abrolhos, supported by the data from each of the coastal blocks, confirms that the exploitation rate has increased to a high level throughout the population, that the accumulated stock has been reduced very considerably, and that the industry is now largely dependent each season upon recruitment by growth into the fishable stock during the preceding closed period. The level of recruitment has decreased, probably due to mortality of undersize crayfish caused either directly or indirectly by their capture in crayfish pots.

The effect of a high exploitation rate on the size composition of the crayfish population should be manifest by a reduction in the relative numbers of large crayfish caught. Some idea of the size composition over the last 10 yr can be obtained from an examination of the number of boxes of crayfish tails in each of the export weight categories received into cold store (see Sheard 1962, for the period 1954–61). These values show no appreciable change but, as Sheard has pointed out, as the fishery has developed the whole stock has not been fished at random but rather with a definite bias. Fishermen initially worked the shallow-water reefs having a high density of relatively small crayfish and later moved into deeper water where larger crayfish predominate. As the fishing pressure increased, fishermen were forced to explore more and more the deep-water reefs and by so doing caught sufficient numbers of large crayfish to maintain the grade category percentages at a steady level, even though the absolute abundance has fallen.

Now that the fishery has passed through the developmental phase expanding the area fished, the high exploitation rate is expected to cause a change in the length frequency of the catch which should be reflected in the percentage composition of the number of boxes of craytails in each grade category. Continuous tests carried out by Sheard (1954) and George (1957) have shown that this does occur if the area of operation remains unchanged. In a test area at the Southern Group, Abrolhos area, commercial fishing during the years 1949–52 reduced the numbers of large crayfish. This is shown by the steepening of the slope of the right hand limb of the 1953 catch curve. (George 1957, figs. 3 and 4).

Taking the catch per unit of effort to be a measure of abundance, we must consider that the fishable stock has now decreased to approximately a quarter of that present some 20 yr ago. If the average exploitation rate for the inner areas of the Abrolhos area in 1963 (62%) is applied to the whole catch of red crayfish in that season, and a lower exploitation rate of 40% assumed for the previous white crayfish season, then the total fishable stock at the commencement of that season was $35 \cdot 5 \times 10^6$ lb of legal-size crayfish. This being so, the original stock (20 yr ago) was of the order of 140×10^6 lb.

From the data shown in Tables 1–9, there is some indication that in those areas which have been heavily fished for some years, the catch per unit effort may be approaching a relatively stable condition where the rate of removal by fishing is approximately in balance with the rate of recruitment. If, for the present level of fishing effort, the stable levels were 1·2 lb per pot-night for the coastal red fishery, 3·0 lb per pot-night for the white fishery, and 2·4 lb per pot-night for the Abrolhos fishery, then the equilibrium catch for the whole fishery might be of the order of 16 million lb ± 2 million lb.

A prerequisite to the establishment of some stable level of fishing is that the pre-recruits should be subject to as little fishing mortality as possible. One approach to this is to keep the fishing effort at a minimum. Recent regulations limiting the number of boats and pots per boat will reduce the mortality of undersize crayfish to some extent. However, still further reduction is needed. The introduction of escape gaps in crayfish pots is considered the best method of achieving this. The protection of the young by means of escape gaps has been applied in the lobster fishery of the southern Gulf of St. Lawrence since 1949 (Wilder 1954). Bowen (1963) has shown that the use of escape gaps reduces the number of undersize red crayfish caught on the shallow-water reefs. Pots with a 2-in. escape gap caught between 50 and 60% less crayfish than a normal pot set on the same grounds. Screening tests have shown that legal-size crayfish cannot be passed through a gap of this size. More recent work (Bowen, unpublished data) has confirmed the results obtained. However, tests made during the white crayfish season resulted in approximately equal numbers of white crayfish being caught in normal and 2-in. escape gap pots. The reason for this was that the length frequency of the undersize fraction of the white population was similar to the length frequency of undersize red crayfish caught in pots with a 2-in. escape gap.

Pots with a $2\frac{1}{8}$-in. gap caught 80–90% less undersize red crayfish and 40% less undersize white crayfish than the normal pots. In a screening test, crayfish of the legal minimum length could be passed through a $2\frac{1}{8}$-in. gap, but the field experiments showed that these small but legal-size crayfish seldom pass through voluntarily. The catches of legal-size crayfish by pots having an escape gap of $2\frac{1}{8}$-in. were as high as (sometimes higher than) the pots with no escape gaps.

Catch and effort statistics now being collected from this fishery are being tabulated for specified areas and depths with sufficient detail to enable more precise assessments of the stock to be made. At the same time, growth, dispersal and recruitment are being studied so that the assumptions inherent in the present model can be checked, and if possible, some prognosis made each year of the level of recruitment which can be anticipated. These studies may reveal that, in spite of the conservation measures adopted and proposed, the fishing pressure is causing the catch per unit effort to continue on a downward trend. If this eventuates a further reduction in the total effort will be required to lower the exploitation rate and consequently the catch.

VII. ACKNOWLEDGMENTS

The model used in the assessment of this stock was developed with the help of Mr. S. J. Holt, Fisheries Division, F.A.O., Rome.

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Paper 16

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LARVAL ECOLOGY OF THE WESTERN AUSTRALIAN MARINE CRAYFISH, WITH NOTES UPON OTHER PANULIRID LARVAE FROM THE EASTERN INDIAN OCEAN

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[*Manuscript received July* 7, 1969]

Summary

The Western Australian marine crayfish is now regarded as *Panulirus longipes cygnus* (George). Larvae could not be distinguished morphologically from those of tropical subspecies. The identity of the various stages of phyllosoma and puerulus larvae of the species has been established, and an outline is given of the seasonal occurrence and growth of larvae. The eggs of *P. longipes cygnus* hatch during summer, larvae being released along the coast into water of relatively high salinity (generally exceeding 35·4‰). Offshore surface wind drift during summer is proposed as the means by which the newly hatched phyllosoma larvae are transported away from the coast. It is not clear how late-stage larvae return to the coast; there is some evidence that their behaviour might change with regard to depth of occurrence and also diurnal vertical movements. The timing of the larval cycle varies from year to year; final-stage larvae probably cannot return to settle on the coast until the disappearance of the low salinity tropical water which extends down the west coast of Australia each winter.

The importance of larval surveys as a means of estimating the size of the brood stock and to forecast the strength of a year class is discussed.

Other species represented in the plankton of this area as phyllosoma larvae are listed, and some information given on the morphology, distribution, and dispersal of phyllosoma larvae tentatively identified as *P. penicillatus*.

I. INTRODUCTION

The marine crayfish or spiny lobster of Western Australia, at present known as *Panulirus cygnus* George, supports a large fishery which exerts a high level of exploitation upon the population (Sheard 1962; Bowen and Chittleborough 1966). Brief descriptions of some larval stages have been given by George (1962), while further stages and times of occurrence of larvae were studied by George and Cawthorn (unpublished data).

In recent years the larval phase has received attention as part of a comprehensive ecological study of this species. The success with which larvae return to settle on the coast at the end of larval life is one of the most important factors in determining the strength of recruitment into the fishable stock. However, little has been known of the extent of larval dispersal, and knowledge of the circulation of water off the west coast of Australia is still being clarified (Rochford 1969), so that the fate of larvae hatching in coastal waters has not been determined.

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II. Material and Methods

The material discussed in this paper was collected from 1962 to 1968, mainly on the oceanographic cruises of H.M.A.S. *Diamantina*, although some plankton was collected from the eastern Indian Ocean by H.M.A.S. *Gascoyne* in 1962 and 1963, and phyllosoma larvae from two plankton stations worked by the oceanographic vessel *Vitiaz* of the U.S.S.R. were kindly made available.

The larvae were collected from a total of 326 plankton stations which were spread from 9°00′S. to 44°36′S., and from the west coast of Australia out to 100°39′E., most of the stations being concentrated nearer to the coast of Western Australia, i.e. from 22°S. to 32°S. and out to 110°E.

The sampling specifically planned for collecting panulirid larvae was either by a 5 ft Isaacs–Kidd midwater trawl or N70 plankton net. Larvae were also obtained from time to time from plankton collected by various other nets used in other programmes.

Depth gauges were attached to the midwater trawls and N70 plankton nets when sampling below the surface. Flowmeters were not used with the midwater trawls, but an estimate has been made of the volume of water filtered during an oblique haul of this net (CSIRO Aust. 1966). During recent cruises the N70 nets were fitted with flowmeters, the readings of which ranged from 10,800 to 35,610 rev. in the standard 30 min hauls at 2–3 kt. The mean of 22,500 rev. is equivalent to approximately 1000 m^3 of water filtered.

III. Panulirid Species of the Area

Breeding populations of seven species of *Panulirus* have been recorded in the eastern Indian Ocean (Sheard 1949; De Bruin 1962; George and Holthuis 1965). Six of these (*P. homarus*, *P. longipes*, *P. ornatus*, *P. penicillatus*, *P. polyphagus*, and *P. versicolor*) inhabit tropical regions. All except *P. longipes* have been taken on the north-west coast of Australia, some extending down to North West Cape (22°S.) but rarely further south, though Bowen (personal communication) has recorded occasional specimens of *P. penicillatus* being taken by trap on the coast at 27°40′S.

P. longipes has been recorded from some of the islands of Indonesia and from Christmas Island, but is is not clear whether this region is occupied solely by *P. longipes longipes* (A. Milne-Edwards) or whether *P. longipes femoristriga* (Von Martens) occurs in some areas. The species may occur around islands off the north-west coast of Australia such as Ashmore Reef, Scott Reef, and Rowley Shoals but there has been no opportunity to verify this.

The panulirid which inhabits the western coast of Australia from 22°S. to 34°S.. supporting a large fishery in the central part of its range, was for many years regarded as a population of *Panulirus longipes* (Milne-Edwards) (Sheard 1949, 1954, 1962; George 1957, 1958*a*; Hodgkin, Marsh, and Smith 1959). In 1962, after comparing specimens from the west coast of Australia with material from other localities in Indo-Pacific waters, George described this Western Australian crayfish as a new species, *P. cygnus*. However, after studying the descriptions of *P. cygnus* and *P. longipes* given by George (1962) and George and Holthuis (1965), and examining fresh and preserved specimens, both of adults and juveniles, from various localities in the Indian and Pacific Oceans, we consider the morphological differences to be very slight and often inconsistent. Differences in colour pattern are more clearly defined, but *P. longipes femoristriga* contrasts in colour pattern much more sharply with *P. longipes longipes* than with *P. cygnus*. Accordingly we propose that the panulirid of the west coast of Australia should be known as *P. longipes cygnus* (George), being an allopatric form close to *P. longipes femoristriga*.

In colour pattern, the pale stripes along the legs of *P. longipes cygnus* are usually less sharply defined than those along the legs of *P. longipes femoristriga*. In early juvenile *P. longipes cygnus* the legs have large pale spots similar to those present on the legs of *P. longipes longipes*.

One morphological feature in which these subspecies appear to differ is that in the adult female *P. longipes cygnus* the pair of spines on the posterior margin of the thoracic sternum (present in juveniles of both sexes and in adult males) are almost worn away, whereas the adult female *P. longipes femoristriga* retains well-developed spines. Although only a few specimens of mated female *P. longipes femoristriga* have been examined, this difference in the spines on the thoracic sternum (of adult females only) may be linked with the positioning of the sperm packets on the thoracic sternum of the female. In *P. longipes femoristriga* the few sperm packets examined had been deposited on either side of the midventral line, whereas in *P. longipes cygnus* the pair of sperm packets overlap, covering the pair of spines which then become eroded either by the enzymes from the sperm mass or the mechanical abrasion applied by the female during spawning.

This apparent difference between the subspecies in the placement of the sperm packets on the thoracic sternum of the female may indicate some genetic difference between the subspecies, but such a difference would not necessarily preclude cross matings. As yet no attempts have been made to compare the viability of eggs fertilized in matings between subspecies.

IV. LARVAE OF THE WESTERN AUSTRALIAN CRAYFISH P. LONGIPES CYGNUS

(*a*) *Identity and Morphology*

Although the Stage I phyllosoma larvae described by George (1962) were hatched from captive egg-bearing females, the late-stage phyllosoma and puerulus larvae were obtained from plankton samples taken off the western coast of Australia, so their identity was inferred from the locality of capture.

During recent oceanographic cruises confirmation of the identity of advanced phyllosoma larvae and of the puerulus phase was obtained by holding live specimens until moulting occurred. Although facilities for holding live specimens on board ship were far from ideal, late stage phyllosoma larvae survived for up to 15 days after capture and appeared to feed when offered living euphausiids, grasping these and holding them to the mouth with the maxillipeds. Freshly dead euphausiids were not accepted by phyllosoma larvae of *P. longipes cygnus*. Two phyllosoma larvae held on the ship moulted to the puerulus phase (11 and 15 days after capture). Although both died immediately after moulting, these moults have enabled late-stage phyllosoma larvae to be linked directly with the puerulus phase.

Two other puerulus larvae of the same species were brought ashore and held in aquaria which contained pieces of limestone reef and its associated benthos. These puerulus larvae, completely transparent when taken by plankton net at the surface at night, sheltered in the algae on the reef fragment throughout captivity, seldom being seen swimming. Feeding was not observed, but after a few days the hepatopancreas became opaque. These specimens became pigmented before moulting, but on moulting (15 and 18 days after capture) the exuviae of the puerulus phase were completely transparent so that the pigment appearing before the moult was being laid down in juvenile cuticle beneath the puerulus exoskeleton. Although the specimens died at the moult, the first juvenile stage could be identified as that of *P. longipes*. As the colour pattern of the adult form was not yet developed in these first-stage juveniles, they could not be assigned to a subspecies.

TABLE 1

SUMMARIZED KEY TO THE IDENTIFICATION OF PHYLLOSOMA STAGES OF PANULIRUS LONGIPES CYGNUS

Character	Stage
1. Eyes unstalked	Stage I
Eyes stalked	2
2. Exopod of 3rd pereiopod not setose	Stage II
Exopod of 3rd pereiopod setose	3
3. 4th pereiopod not segmented	Stage III
4th pereiopod segmented	4
4. Exopod of 4th pereiopod not setose	Stage IV
Exopod of 4th pereiopod setose	5
5. Antennule segments incomplete	Stage V
Antennule segments complete 2–1–1	6
6. Uropods not bifid	Stage VI
Uropods bifid	7
7. Abdomen not segmented; pleopods not bifid	Stage VII
Abdomen segmented; pleopods bifid	8
8. Uropods without lateral spines	Stage VIII
Uropods with lateral spines	9
9. Gills present; pleopods with appendix interna	Stage IX

Mid-stage phyllosoma larvae taken at sea died soon after capture so that it has not been possible to link each stage by an observed series of moults. However, of the graded series of developmental stages obtained from the plankton, the first and last larval stages have now been linked to the adult form, so that the specific identity of these larvae is well defined.

Eleven morphological stages of phyllosoma larvae have been described for *Panulirus argus* (Lewis 1951), and *P. interruptus* (Johnson 1956), and indicated also for *P. penicillatus* (Prasad and Tampi 1959). At the commencement of this project an attempt was made to apply a similar 11-stage key developed by George and Cawthorn (unpublished data) for phyllosoma of *P. longipes cygnus*. However, because of individual variations in the sequence in which certain morphological features appear, and in the rate of development of some appendages, difficulty was often experienced in assigning specimens to a particular stage. After examining several hundred phyllosoma larvae of this species a simplified nine-stage key was produced (Table 1), based on very clearly defined morphological features which appear in sequence during larval development.

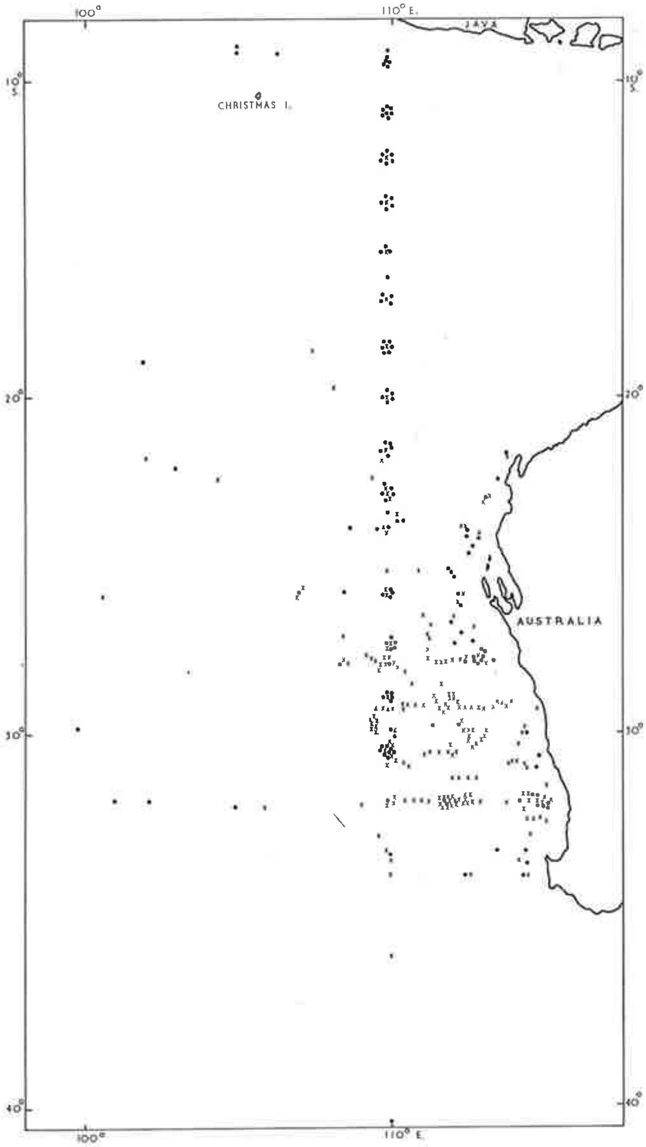

Fig. 1.—Locations of net stations at which larvae of *P. longipes* were taken (×) or absent (●) on oceanographical cruises during 1962–68.

Although these stages succeed each other in the order given, they should not be regarded as single instars. Johnson and Knight (1966) and Saisho (1966*a*) have emphasized this, pointing out that "stages", while useful for ecological studies of phyllosoma larvae, represent only the more obvious morphological changes which occur during a relatively rapid series of moults. Thus during any one stage there could be several moults (and not necessarily a constant number of moults), each of which involves little morphological change, as demonstrated by the aquarium studies of Inoue and Nonaka (1963) upon phyllosoma larvae of *P. japonicus*. In the development of blue crab larvae, Costlow (1965) observed that moulting of a larva may result in (1) no perceptible morphological change, (2) missing of a stage previously described, (3) a combination of morphological characteristics previously described for two separate larval stages.

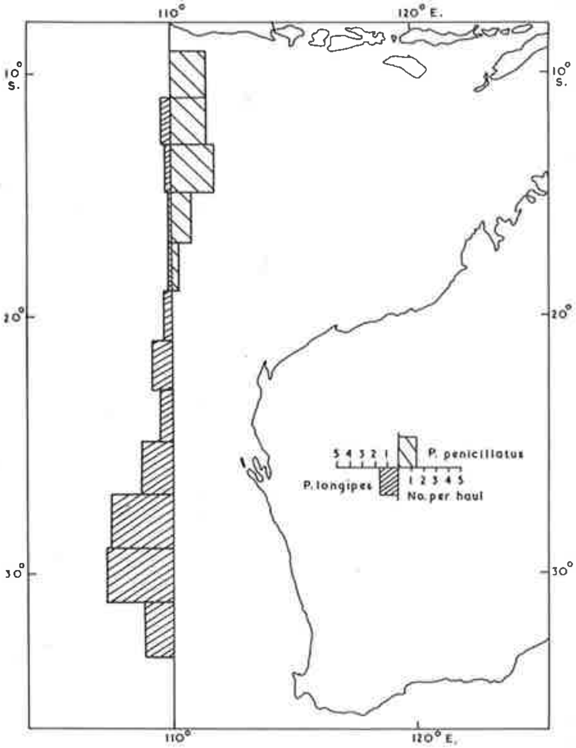

Fig. 2.—Relative abundance of phyllosoma of *P. longipes* and *P. penicillatus* along 110°E. meridian during 1962 and 1963.

Although the nine stages of phyllosoma larvae of *P. longipes cygnus* described here are somewhat arbitrary, and the average duration of each stage has not been determined, they do enable an approximate time sequence to be applied to the collections of larvae of this species.

(*b*) *Distribution*

The distribution of larvae of *P. longipes* recorded from the plankton stations considered in this report is shown in Figure 1. Some of these larvae were far to the north of the adult stock of *P. longipes cygnus*. The relative abundance of phyllosoma larvae of *P. longipes* along the 110°E. meridian from 9°S. to 33°S. is indicated from a series of oblique hauls of a midwater trawl made at the same time each night, from 200 m to surface (Fig. 2). Although this was a relatively inefficient method of sampling these larvae (which are usually concentrated at the surface during the night), the catch rates illustrated in Figure 2 for *P. longipes* show a peak from 27°S. to 31°S., due west of the adult population of *P. longipes cygnus*, and a small secondary peak round 12°S., in the region of the South Equatorial Current (Rochford 1962). Although these phyllosoma larvae from tropical waters were not distinguishable from the larvae of *P. longipes cygnus*, they are most unlikely to have come from the breeding stock on the lower west coast of Australia. They are more likely to be larvae of the tropical subspecies of *P. longipes* from the islands of Indonesia. If this was so, it would bring the total number of panulirid species represented as phyllosoma in the tropical stations to six, which is consistent with the six species known to inhabit that region (Section III).

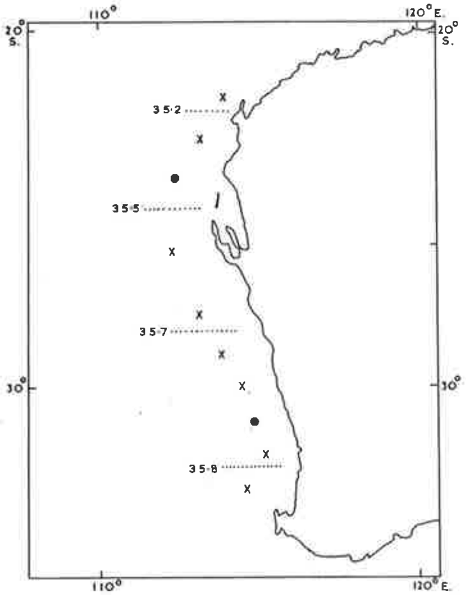

Fig. 3.—Plankton stations at which early larvae of *P. longipes cygnus* were present (+) and absent (●) during *Diamantina* cruise 1/64 of January 29–February 18, 1964. Surface salinity levels shown (.......).

As a prerequisite to a study of the ecology of larvae of *P. longipes cygnus*, it is necessary to separate these from the larvae of the tropical subspecies. The larvae could not be distinguished morphologically, but might be separated on the basis of the characteristics of the water in which they occur.

Larvae of *P. longipes cygnus* hatch during the summer (George 1958*b*) along the west coast of Australia between 22°S. and 34°S. At the time of larval release, the salinity of coastal water increases with latitude (Fig. 3). At the northern part of the range of the subspecies (22°S.), some larvae are released into water of salinity of 35·2‰. There is no doubt that these newly hatched phyllosoma found close to the coast at 22°S. are *P. longipes cygnus*, the nearest known occurrence of tropical subspecies of *P. longipes* being at Christmas Island (10°30′S., 105°40′E.). Most of the adult stock of *P. longipes cygnus* is concentrated between latitudes 27°S. and 32°S., so that in 1964 (Fig. 3) most of the larvae of this subspecies would have been released into waters whose salinity ranged from 35·6 to 35·8‰. Because of variations in salinity along this coast from one summer to another (Rochford 1969, Fig. 1), the majority of the larvae of this subspecies are released into waters having a salinity range from 35·4 to 36·0‰.

Larvae of the tropical subspecies of *P. longipes* are released into water having a salinity of 35·0‰ or less, specimens having been taken in waters whose salinity was as low as 34·2‰ (Fig. 4).

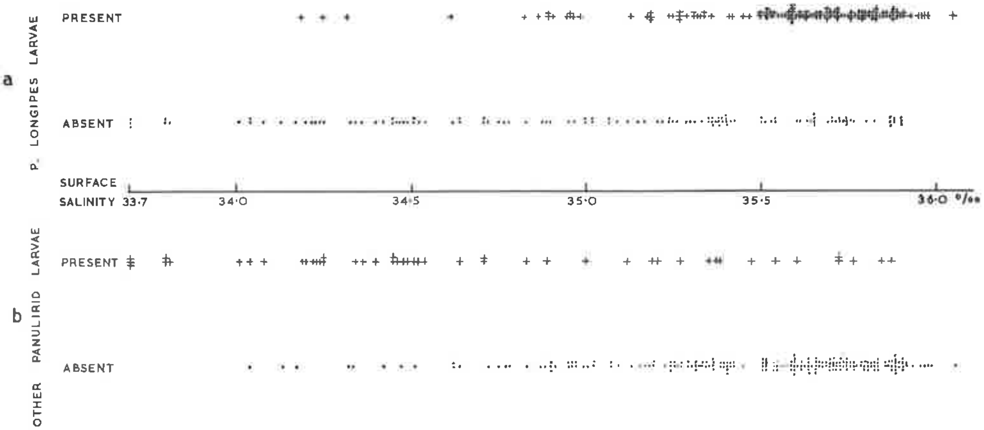

Fig. 4.—Surface salinity at each plankton station in the eastern Indian Ocean, showing those at which (*a*) *P. longipes* larvae, (*b*) other panulirid larvae, were present or absent.

While mixing of low salinity tropical water and high salinity subtropical water might make the identity of larvae within such mixed water less certain, there is very little doubt that all larvae of *P. longipes* taken in water whose salinity exceeded 35·4‰ were of the subspecies *P. longipes cygnus*. On this basis the present material includes 9250 larvae of the Western Australian crayfish and 83 specimens predominantly of a tropical form. The latter group might well include a few individuals of *P. longipes cygnus*, but for present purposes this is not important.

The developmental stages of the larvae of *P. longipes cygnus* have been recorded in each month (Table 2). Although these are pooled results from a variety of gear sampling at different times of the year over seven years, there is a general trend from first-stage phyllosoma larvae at the beginning of the year to final stages towards the end of the year.

(*c*) *Dispersal*

(i) *Offshore Movement of Larvae*.—Due to absence of oceanographical vessels, no sampling of plankton was made from mid November to the end of January, so the full season of larval release of *P. longipes cygnus* was not covered by these cruises. In most years, larvae are still hatching along the west coast of Australia towards the end of summer (e.g. Fig. 3). By autumn these phyllosoma larvae are displaced further offshore. The flow of low salinity tropical water shown by Rochford (1969) to extend down the west coast of Australia during the latter part of autumn each year might help to displace the larvae away from the coast. However, offshore movement of larvae takes place during summer and autumn before the coastal influx of tropical water. This offshore movement of phyllosoma larvae is now considered to be brought about by surface wind drift.

TABLE 2

NUMBERS OF LARVAE OF P. LONGIPES CYGNUS FROM SALINITIES ABOVE 35·4‰, TAKEN IN EACH MONTH (1962–1968)

Month	Phyllosoma Stage I	II	III	IV	V	VI	VII	VIII	IX	Puerulus
Jan.	2			2	4					
Feb.	144	144	96	78	651	1497	7	5	15	1
Mar.	3	85	173	418	2652	2395	6		3	2
Apr.					3	16	8	2		
May				1	11	304	4	1		
June						2	1			
July					1	83	27	19	1	1
Aug.					3	7	12	4	1	
Sept.							4	1	1	
Oct.					2	3	8	17	15	2
Nov.						25	79	119	64	5
Dec.										

A typical feature of the summer weather pattern in this region is a low pressure trough extending down the western coast, associated with an anticyclone to the south of Australia (Fig. 5). This pattern maintains an offshore airflow to the west of Australia, temporarily replaced by a more southerly air stream when the low pressure trough crosses the western coast.

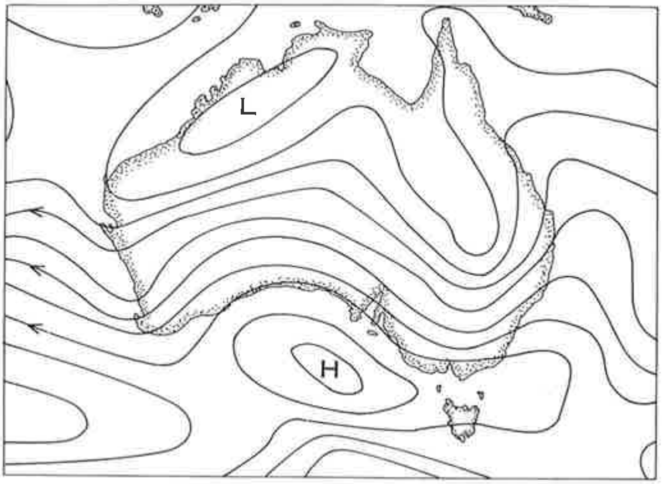

Fig. 5.—Meteorological chart showing typical summer pattern resulting in an offshore flow of air along the western coast of Australia.

On the coast at Fremantle, the daily wind pattern during summer generally consists of a wind from the south-south-east during the early hours (Table 3), becoming more easterly from sunrise, then swinging to south-south-west and south-west rather abruptly late in the morning. This sea breeze usually continues quite strongly during the afternoon (ranging from 7 to 28 kt, mean 17 kt), swinging in the evening through south (12–33 kt with a mean of 19 kt), becoming south-south-east by about midnight. When the weather pattern typified by Figure 5 is strongly developed, the coastal sea breeze fails to develop in the afternoon, so that an easterly (offshore) air flow is maintained for several days.

Table 3

FREQUENCY OF OCCURRENCE OF WIND DIRECTION THROUGHOUT THE DAY AT FREMANTLE (32°03′S., 115°44′E.) FOR EACH OF THE 31 DAYS OF DECEMBER 1967

From hourly records maintained by the Fremantle Port Authority

Wind	Hour of Day																							
Direction	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
N.					1	1			2															
NNE.																								
NE.						1	2	1		1			1			1				1	1			
ENE.	1	1	1	2	2	2	3	5	4	4	3	3	1	1	1									
E.	3	2	4	2	6*	7*	6*	7*	6*	4	3	3	1					1	2	2	2	3	4	4
ESE.	4	5	3	7*	6*	5	4	2	2	1	1		1	2				1						
SE.		1	2	2		2	2	2	2	2				2			1		2	1	1	1		2
SSE.	6*	8*	6*	6	5	4	4	5	3	1											1	1	3	4
S.	5	4	5	2	3	1	3	3	4	2	1					1	1	1	1	1	6	9	10*	9*
SSW.	4	3	3	3	2	3	2	2	3	8*	9*	9*	9	9	14*	14*	16*	17*	17*	16*	13*	10*	7	5
SW.	3	2	2	2	2	2	1	1	1	2	5	6	10*	10*	10	9	7	6	4	2	2	1	1	1
WSW.	1	1	1							1	3	2	2	4	2	2	1	1	1	1	1	2	2	2
W.				1	1							3	1		1		2	2	3	2	3	1	1	1
WNW.	1	2	2	1	1	2	2	1	1	1	2	2	2	3	1	3	2	1	1	2	1	2	2	1
NW.	2	2	2	3	2	1	1	2	1		1	1	2	1	2	1	1	1				1	1	2
NNW.	1								2	3	2	1	1											
Total days	31	31 etc.																						

* Wind direction occurring most frequently at that hour, during December 1967.

Newly hatched larvae, present at the surface throughout the night, are exposed to the effects of winds mainly from the east and south. Although a southerly wind in the early part of the night is blowing parallel to the coast, this would generate an offshore surface drift owing to the Coriolis force deflecting surface water up to 45° to the left in the southern hemisphere (Sverdrup, Johnson, and Fleming 1942).

If the western coast of Australia is taken as a straight line extending north and south, then winds from the south-west and north-east will generate surface wind drift parallel to the coast, while a south-east wind will generate an offshore surface wind drift at right angles to the coast. The wind records maintained hourly at Fremantle record the wind direction as one of 16 points of the compass, so that the component producing an offshore surface wind drift has been calculated by multiplying the wind velocity in each hour by the following vectors:

SW.	SSW.	S.	SSE.	SE.	ESE.	E.	ENE.
0·0	+0·38	+0·70	+0·92	+1·0	+0·92	+0·70	+0·38
NE.	NNE.	N.	NNW.	NW.	WNW.	W.	WSW.
0·0	−0·38	−0·70	−0·92	−1·0	−0·92	−0·70	−0·38

Using this method, Figure 6 shows that for December the total offshore wind component is relatively high throughout the hours of darkness, falling almost to zero round midday. Such a consistent offshore wind component would be sufficient to produce an offshore drift of surface water. If a conversion factor of 5% is applied to the total offshore wind component from 2100 hr to 0400 hr of each night during December 1967, the wind data shown in Figure 6 would have caused an offshore surface drift of 73 nautical miles during that month (for the hours of darkness). This represents the maximum distance that newly hatched phyllosoma larvae could have moved offshore during that month if the larvae were at the surface each night, and were below the depth of wind induced movement during daylight.

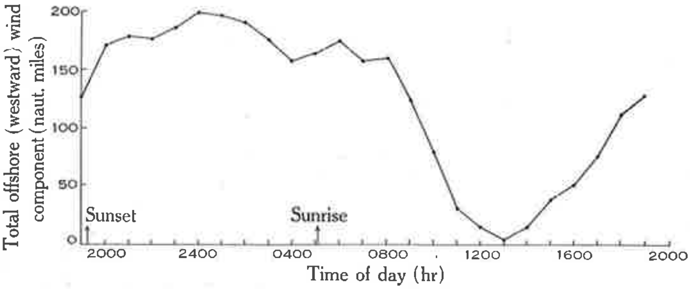

Fig. 6.—Total nautical miles of offshore (westward) wind effect hour by hour for the whole of December 1967 at Fremantle (32°03′S., 115°44′E.).

Table 4 shows that the offshore surface wind drift at night increases during the spring and is generally high throughout the summer, being strongest in January. The values calculated for October are low; in fact, the offshore wind components for each hour are so small (sometimes being onshore) that it is doubtful whether an offshore drift of surface water would be generated in that month. This also applies to November 1965, when the offshore drift as calculated was again very low (Table 4).

Table 4

ESTIMATES OF TOTAL OFFSHORE (WESTWARD) SURFACE WIND DRIFT (NAUTICAL MILES) AT NIGHT (2100–0400 HR) THROUGHOUT SELECTED MONTHS AT FREMANTLE

	Oct.	Nov.	Dec.	Jan.	Feb.
1967–68	23	60	73	92	58
1965–66	9	17	35	95	71
1963–64	21	47	51	67	67

Plankton hauls taken near the edge of the continental shelf in late summer collected early phyllosoma larvae of *P. longipes cygnus*, stations a few miles further offshore showing slightly more developed stages (Table 5). At this time of the year the larvae have generally not drifted far offshore. However, in February 1968, the phyllosoma larvae of this species were in far more advanced stages of development than at the same time in previous years (Table 6). Also the larvae were dispersed

TABLE 5

LARVAE OF P. LONGIPES CYGNUS TAKEN IN THREE CONSECUTIVE PLANKTON TOWS* NEAR THE EDGE OF THE CONTINENTAL SHELF ON THE NIGHT OF FEB. 15–16, 1966, AT 32°S.

Miles West of Shelf Edge	Phyllosoma Stages			
	I	II	III	IV
3	43	17	1	
6	20	28	15	
9	11	21	14	1

* 30 min horizontal surface hauls of N70 net at 2½–3 kt.

much further offshore in February of 1968 than at the same time in previous years, stations near the edge of the continental shelf generally producing few or no larvae in February 1968 (Fig. 7). One area not far from the shelf contained relatively high densities of larvae, but again these larvae were of more advanced stages than those found at the same period in previous years.

TABLE 6

LARVAE OF P. LONGIPES CYGNUS TAKEN OFF WESTERN AUSTRALIA DURING FEBRUARY IN RECENT YEARS

Year	Phyllosoma Stage									Puerulus
	I	II	III	IV	V	VI	VII	VIII	IX	
1964	69	56	20	21	4	1				1
1966	74	70	30	1						
1968	1	18	46	56	647	1496	7	5	15	

During the spring of 1967 the monthly mean temperature of coastal water in this region was consistently above corresponding values in earlier years (Table 7). Aldrich (1967) showed that the incubation period of marine crayfish eggs is shortened at higher temperatures. Then the hatching of larvae would have been earlier in 1967–68 than in previous seasons, so that by February of 1968 the larvae would have reached more advanced stages than attained in the same month during previous years.

TABLE 7

MEAN SURFACE WATER TEMPERATURE (°C)* AT KWINANA, COCKBURN SOUND, IN SPECIFIED MONTHS

Month	1963	1964	1965	1966	1967
Sept.	16·2	16·8	16·6	16·0	17·5
Oct.	18·5	17·2	18·0	17·0	19·7
Nov.	20·2	19·1	19·1	20·1	21·1
Dec.	22·5	20·6	22·8	21·8	22·5

* From maximum and minimum temperature recorded daily.

If in 1967, larvae of *P. longipes cygnus* had begun hatching at the beginning of November, they would have been exposed to nearly four months of relatively strong offshore surface wind drift by the time they were sampled towards the end of February 1968. From the estimates of surface drift given in Table 4, larvae could have been carried up to 280 miles westward during that time. This is consistent with the distribution of larvae shown in Figure 7.

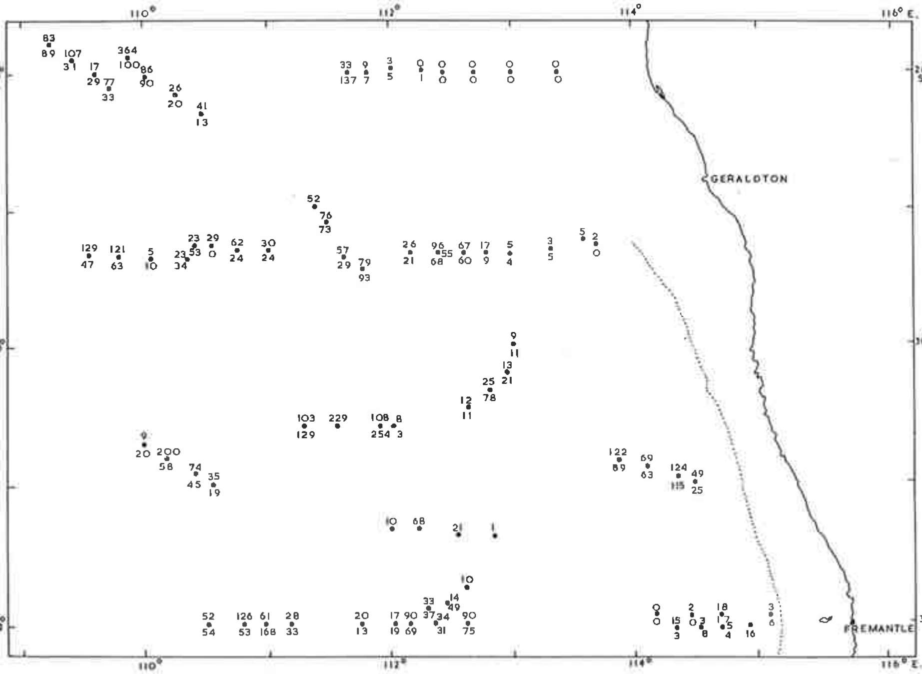

Fig. 7.—Relative densities of larvae of *P. longipes cygnus* in surface water at night during *Diamantina* Cruise 1/68 (Feb. 19–March 10, 1968). Numbers of larvae taken in consecutive half-hour horizontal tows of N70 plankton net converted to catch per 22,500 rev. of flowmeter (= approximately 1000 m^3 water filtered). Upper figures, first haul; lower figures, second haul.

During *Diamantina* Cruise 1/68, winds were strong, continuous, and mainly from the south-south-east and south, even out at 109°E., so that the offshore surface wind was continuing to operate during February and March 1968 at over 250 miles from the west coast of Australia.

Relatively few of the plankton stations were situated to the west of 109°E., so that little is known of the extent of offshore dispersal of larvae of *P. longipes cygnus*. A line of stations extending westward from the coast along 32°S. during May 1966 (Table 8) showed at that latitude a concentration of phyllosoma larvae at 110°07′E., and relatively few to the west of that station. However, further north (at 26°S.), larvae of this species were relatively common at the same time (May 14, 1966) at a station on 100°39′E., 700 miles from the coast of Australia, successive plankton tows (made under the same conditions as those in Table 8) taking 27 and 10 phyllosoma larvae of *P. longipes cygnus*.

TABLE 8

NUMBERS OF P. LONGIPES CYGNUS PHYLLOSOMA TAKEN ALONG 32°S. BY 30 MIN HORIZONTAL SURFACE HAULS OF N70 NET (3 KT) AT NIGHT, MAY 9–12, 1966

Longitude:	113°48′E.	112°56′E.	110°07′E.	109°08′E.	105°53′E.	105°00′E.	102°10′E.	101°05′E.
Miles offshore:	100	145	290	340	520	565	710	760
Catch per haul:								
Haul 1	4	2	76	4	3	0	0	0
Haul 2	1	—	154	—	1	—	—	—

(ii) *Return of Larvae to Coast*.—Little is known of the means by which larvae of this species return to the coast. The small quantity of data obtained during the spring indicated that the phyllosoma larvae are moving (or being moved) back towards the west coast of Australia, but the mode of transport is not known. During the spring the larvae nearer the coast tend to be slightly more advanced in their development than larvae further offshore (Table 9). This contrasts with the situation during the offshore movement earlier in the year when the larvae furthest from the coast were the more advanced in their development.

TABLE 9

DEVELOPMENTAL STAGES AND DISTANCE OFFSHORE OF LARVAE OF P. LONGIPES CYGNUS TAKEN BY PLANKTON NET FROM OCTOBER 30 TO NOVEMBER 13, 1967

Larval Stage	0–70 Miles	70–140 Miles		140–210 Miles		210–280 Miles		280–330 Miles*	
	No.	No.	%	No.	%	No.	%	No.	%
Phyllosoma									
Stage VI	0	1	1·7	1	2·6	5	13·5	17	16·3
Stage VII	3	1	1·7	10	26·3	6	16·2	47	45·2
Stage VIII	0	28	48·3	20	52·6	13	35·1	33	31·7
Stage IX	2	27	46·6	5	13·2	12	32·4	7	6·7
Puerulus	1	1	1·7	2	5·3	1	2·7	0	0

* Distance offshore.

(*d*) *Diurnal Vertical Movement*

During two cruises diurnal vertical migrations were studied by means of stratified horizontal sampling at various depths throughout at least 24 hr at the one locality. An N70 plankton net was used for the surface sampling, and 5 ft Isaacs–Kidd midwater trawls for the subsurface sampling. Two midwater trawls, attached at different points to the one warp, were closed at the end of each tow by messengers releasing the upper bridle of each net. This closing mechanism sometimes failed on one or both nets, so that the resulting oblique hauls had to be deleted from the series.

The first of the 24 hr stations was in March 1966 at 29°S., 112°E., where mid-stage (IV–VI) phyllosoma larvae were relatively abundant. Figure 8 shows that these larvae were relatively dense at the surface during the night and that a few were still present at the surface during daylight hours. Subsurface sampling (from 40 to 190 m) indicated that phyllosoma larvae were of low density both night and day. The thermocline at 50–70 m did not appear to act as a barrier to vertical diurnal movements; aggregations of phyllosoma larvae were not found immediately above or below it during the 24 hr period.

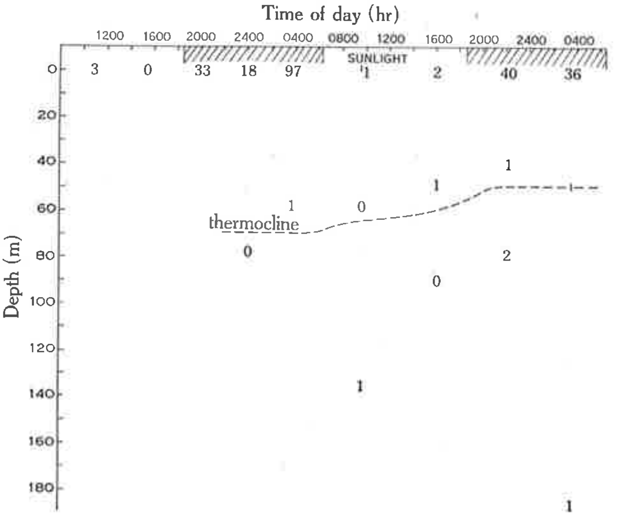

Fig. 8.—Distribution of phyllosoma of *P. longipes cygnus* with time and depth, at 29°S., 112°E. on March 18–20, 1966. Catches converted to approximate densities (number per 1000 m³).

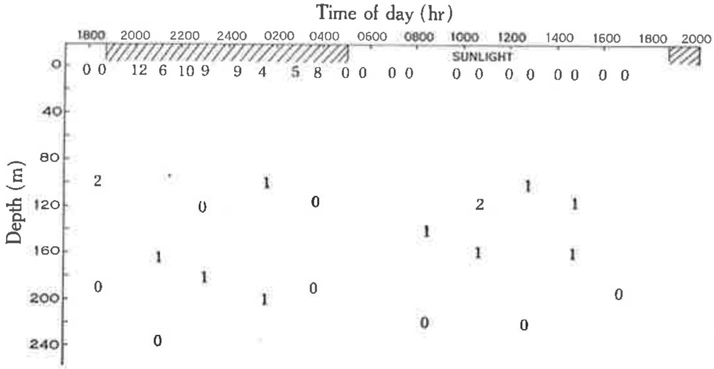

Fig. 9.—Distribution of phyllosoma of *P. longipes cygnus* with time and depth, at 30°S., 109°30′E. on November 4–5, 1967. Catches converted to approximate density (number per 1000 m³).

Figure 9 summarizes the results for the second of the 24 hr stations, occupied at 30°S., 109°30′E. in November 1967, when later stages (VI–IX) of phyllosoma larvae were present. In the absence of a thermocline in the upper 300 m of water, subsurface hauls were made at greater depths than in the series of March 1966. Larvae were again present in surface water at night, though not in high concentrations. During daylight hours no larvae were caught at the surface, in contrast with the finding of some earlier stages at the surface in daylight during March. Apparently the more advanced phyllosoma larvae of this species are more strongly negatively phototropic than the earlier stages. Subsurface sampling showed very low densities, but there were indications of slightly more phyllosoma at 100–180 m during daylight hours than at night. Very few larvae were taken in the deeper hauls (180–240 m).

From the rather limited data available, there appears to be some difference between the mid and late stages of phyllosoma larvae of this species in their diurnal vertical migrations. Of the mid-stage larvae taken in March, the frequency of occurrence of the different stages was the same for surface (N70 plankton net) and subsurface (midwater trawl) samples (Fig. 10(*a*)): $\chi_3^2 = 0\cdot9068$ ($P > 5\%$). However, from the catches of late-stage larvae taken in November (Fig. 10(*b*)), final-stage phyllosoma larvae were less well represented at the surface than in subsurface samples, $\chi_1^2 = 5\cdot32$, $P < 5\%$, indicating that towards the end of the phyllosoma phase there is a difference in the frequency of occurrence of the stages between surface and subsurface samples. This could be of importance to the return of phyllosoma larvae towards the west coast of Australia, the final stages moving more often at some subsurface level. However, eastward movement of subsurface water, at a speed sufficient to return these late-stage larvae to the coast, has yet to be demonstrated.

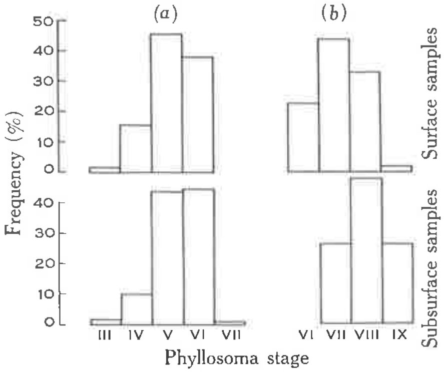

Fig. 10.—Distribution of stages of *P. longipes cygnus* phyllosoma taken at the surface (by N70 plankton net) and subsurface net (by midwater trawl): (*a*) 24 hr station, Mar. 19–20, 1966; (*b*) 24 hr station, Nov. 4–5, 1967.

To test an hypothesis that late-stage larvae returned to the coast in relatively deep water and settled on the outer part of the shelf, and the early juveniles then walked into shallow waters, several cruises were made along the edge of the shelf sampling the water just above the continental slope and shelf (by midwater trawl) and also sampling the benthos (by beam trawl and dredge). No larvae or early juveniles of *P. longipes cygnus* were obtained, but some puerulus phase were taken by plankton net in the surface water.

When the Stage IX plyllosoma larva moults into the puerulus phase, the latter apparently returns to the surface, as collectors buoyed along the coast gather puerulus larvae much more effectively when at the surface than collectors only 3 m below the surface (Phillips, personal communication). Sheard (1949) stated that the puerulus phase of this species is positively phototropic, staying in surface water layers.

(*e*) *Growth*

The duration of larval life extends over approximately 11 months (Table 2), most of which is occupied by a succession of moults through the phyllosoma phase.

Growth through the nine rather arbitrary stages of phyllosoma larvae is shown in Figure 11. Since the morphological stages do not necessarily represent equal units of time, a growth curve cannot be derived from these data. Progression through these stages is relatively rapid to Stage V, generally being achieved in some three months, after which morphological changes are much slower.

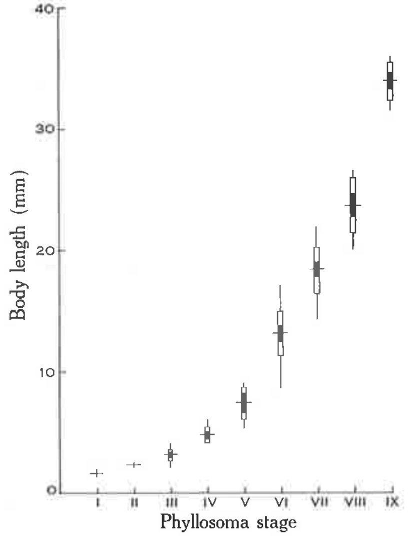

Fig. 11.—Total body length of each stage of phyllosoma of *P. longipes cygnus*. Vertical line shows observed range; horizontal gives mean length; black bar extends two standard errors on each side of mean; hollow bar ends one standard deviation on each side of mean.

On some occasions, wide differences in stage of development of phyllosoma larvae have been recorded from two stations sampled within a few days of each other (e.g. Table 10). This probably reflects different times of hatching rather than differing rates of growth.

Table 10

NUMBERS OF PHYLLOSOMA OF P. LONGIPES CYGNUS WITHIN EACH GROWTH STAGE, OBTAINED AT TWO ONSHORE STATIONS BY THE SAME GEAR DURING MARCH 1966

Stn. No.	Date	Lat. S.	Long. E.	Surf. Temp. (°C)	Surf. Salin. (‰)	Phyllosoma Stages I	II	III	IV	V	VI
15	Mar. 6	30°21′	114°11′	22·5	35·89	0	1	6	30	82	21
29	Mar. 9	26°58′	112°43′	22·6	35·72	1	77	46	15	1	0

Quite distinct from this are differences which have been observed in the sizes attained at particular stages. These were most marked in the case of Stage VI phyllosoma larvae, the mean length of specimens at this stage being lower early in the year than of those reaching this stage later in the year (Table 11).

As the hatching of larvae is virtually completed by the end of February, there is no doubt that the Stage VI phyllosoma larvae taken in November had a much slower rate of development (though reaching greater size) than those reaching the same stage in February or March.

TABLE 11

LENGTHS OF STAGE VI PHYLLOSOMA OF P. LONGIPES CYGNUS SAMPLED IN VARIOUS MONTHS OFF THE WEST COAST OF AUSTRALIA

Month	No. Measured	Body Length (mm)			
		Min.	Max.	Mean	S.D.
Feb. 1968	316	8·3	15·0	10·4	1·3
Mar. 1966	30	9·3	15·5	11·8	1·9
1968	298	8·3	15·0	10·7	1·3
May 1966	92	8·4	18·1	13·8	1·8
July 1965	30	13·3	17·8	15·8	1·3
Nov. 1967	23	11·9	17·9	15·8	1·4

At full development, phyllosoma larvae of *P. longipes cygnus* ranged from 31·5 mm to 35·9 mm with a mean length of 33·9 mm, standard error 0·3 mm (17 specimens measured).

V. LARVAE OF P. PENICILLATUS

(*a*) *Identity and Morphology*

Amongst the material collected were 122 phyllosoma larvae of the same species as those larvae listed by Prasad and Tampi (1959) as *P. penicillatus*. The identity of these larvae has not yet been verified by direct observations such as the hatching of eggs from the female or observing the final stage phyllosoma larva to moult to the puerulus phase and first juvenile phase. In fact, Michel (personal communication) questions the identification given by Prasad and Tampi, having found that at New Caledonia and also around the Tuamotu Archipelago (near Tahiti), where *P. penicillatus* is the most plentiful panulirid species as adults, the phyllosoma larvae abundant in the plankton are not what was described by Prasad and Tampi as larvae of *P. penicillatus*.

Although there is this uncertainty, the name *P. penicillatus* will be retained for present purposes as we wish to add to the description of morphological stages given by Prasad and Tampi.

In their morphological stages for phyllosoma larvae of *P. penicillatus*, Prasad and Tampi noted that they did not have specimens of Stage VIII. Fourteen specimens of this missing stage were found in the present series. In addition, 15 specimens were more advanced than Stage X of Prasad and Tampi, so have been assigned to an additional Stage XI. Brief descriptions of these two stages are as follows:

Stage VIII.—Total body length 11·7–14·1 mm, mean 13·4 mm (14 specimens). The exopod bud of the second maxilliped is segmented at the base and has become setose. The uropods are bifid. The pleopods appear as low crescentic buds. The hindbody is a little wider than the forebody. Ventrally on the hindbody there is a small spine adjacent to the coxa of each periopod and of the third maxilliped. The abdomen has increased in length and is widest at the base. On the antennule the endopod bud is extended but not articulated. The second maxilla has expanded to a leaf-like appearance. The fifth pereiopod is half the length of the abdomen. There is a ventral coxal spine on the first pereiopod and third maxilliped only. Dorsal coxal spines are present on pereiopods 2, 3, and 4, but are rudimentary or absent on 1 and 5. One to three small spines are irregularly spaced dorso-ventrally along the merus of each pereiopod.

Stage XI.—Total body length 22·2–30·2 mm, mean 25·5 mm (15 specimens). Forebody wider than hindbody; hindbody with a spine ventrally adjacent to the coxa of each pereiopod and of the third maxilliped. Antennae one and a half times the length of eyestalk and eye. Antennule half the length of the antenna. First maxilliped has become trilobed; second maxilliped with a setose exopod; third maxilliped has three spines equally spaced along the merus dorso-ventrally; pereiopods 1, 2, and 3 usually have two or three spines similarly placed. Dorsal and ventral coxal spines present on all pereiopods and a large curved spine on the terminal joint of the merus. Pleopods have an appendix interna. Uropods have a lateral spine. The fifth segment of the abdomen has a pair of large spines posterio-laterally, directed rearwards horizontally. Gills are present on the third maxillipeds and all pereiopods.

During the growth of these phyllosoma larvae, the sequence of appearance of various morphological features is quite variable so that there can be considerable overlap from one of these somewhat arbitrary stages to another. However, the determining features for Stage VIII are quite constant. These are the segmentation of the exopod on the second maxilliped and the bifid appearance of the uropods. For Stage XI the characteristic features are the appendix interna on each pleopod and the gills present on maxillipeds and legs. The lateral spines on the uropods may be rudimentary in some specimens.

(*b*) *Distribution and Dispersal*

Most of the phyllosoma of *P. penicillatus* were found north of 20°S. (Fig. 2). Only two isolated specimens were found well offshore off the west coast of Australia. Inshore, seven specimens were taken close to North West Cape (at 22°34′S., 113°32′E.), close to the southernmost point on this coast where adults of tropical panulirids are commonly found. Five specimens found close to the coast at 32°S. during May, July, and August might well have been swept southwards by the coastal current known to move down the coast during winter months.

Figure 2 shows that larvae of *P. penicillatus* were of highest density in the vicinity of 10°S.–15°S., in which region the South Equatorial Current carried surface water westward (Rochford 1962). On this basis, it might be suggested that phyllosoma larvae of this species are carried westward on the South Equatorial Current, returning via the Equatorial Counter Current along the coast of Java. However, further westward, in the region of 78°E. to 98°E., Saisho (1966*b*) found phyllosoma larvae of the same species to be common in the vicinity of the equator but none south of 10°S., so that they were absent from the South Equatorial Current in that region. Larvae of this species present near the 110°E. meridian appear then to be largely independent of the prevailing surface current, perhaps by spending a considerable portion of each day below the thermocline.

(c) *Seasonal Cycle and Growth*

Table 12 shows no indication of a seasonal cycle in the appearance of early-stage phyllosoma larvae of *P. penicillatus* and subsequent progression during following months to late-stage larvae. This indicates that spawning can occur throughout the year as would be expected for a tropical species.

TABLE 12

NUMBERS OF P. PENICILLATUS PHYLLOSOMA IN STAGES TAKEN IN EACH MONTH

Month	Stage								
	III	IV	V	VI	VII	VIII	IX	X	XI
Jan.					1	2		2	
Feb.							1		
Mar.	1		2	2			2	1	
Apr.			1	5	4	6	2	3	5
May		1	1	4	7	3	1	3	7
June									
July		1						5	
Aug.		1	5	2	4	3	4	3	4
Sept.			2		2	2	1	1	1
Oct.						1	1	1	2
Nov.			2	2	3	1			1
Dec.									
Total (122)	1	3	13	15	21	18	12	19	20

Along the 110°E. meridian, while a wide range of larval stages are present near Java, i.e. at 9°S., the range of stages narrows so that only late-stage phyllosoma larvae are present further south (Table 13).

TABLE 13

NUMBERS OF P. PENICILLATUS PHYLLOSOMA OF EACH STAGE TAKEN ALONG 110°E. MERIDIAN

Latitude	Phyllosoma Stages							
	IV	V	VI	VII	VIII	IX	X	XI
9°S.	3	5	4	6	4		3	3
10°S.		2		1				
11°S.		4	4	4	1	1		1
12°S.			5	1	3	2	4	7
13°S.								
14°S.			3	4	6	5	3	5
15°S.				1	2		3	1
16°S.								
17°S.							1	1
18°S.							1	

Although the evidence is somewhat circumstantial, it might be inferred from Figure 2 and Table 13 that there is a relatively large breeding stock of this panulirid species around the islands of Indonesia.

VI. Other Species Represented by Phyllosoma

Phyllosoma larvae of four other species of *Panulirus*, including species A and B of Gurney (1936), were taken from these stations, mainly from low salinity tropical waters as was anticipated since the other panulirid species of the area are tropical (see Section II).

In addition, the following genera were represented by phyllosoma larvae:

Palinurus, two species;
Palinurellus, one species;
Parribacus, one species;
Jasus, one species;
Thenus, two species;
Scyllarus, five species;
Scyllarides, two species;
Phyllamphion, one species.

There is also one specimen from a genus not described by Gurney.

Some of these larvae were quite restricted in their range, apparently reflecting the range of the adult population of that species. In some cases large numbers of specimens were present, spanning several growth stages. Each stage is being described and figured in the hope that later it will be possible to link early stages with early larvae hatched from egg-bearing females held in aquaria, so that the species can be identified with certainty.

Some late-stage scyllarid larvae held in aquaria moulted, but not into juveniles which could be identified. A mid-stage phyllosoma larva moulted to a later stage after being held and fed for 25 days. Several late-stage phyllosoma larvae moulted only four days after capture, remaining in the phyllosoma phase. Scyllarid phyllosoma larvae accepted freshly killed as well as living euphausiids offered as food, in contrast to the larvae of *P. longipes cygnus* which would only accept living material. Two late-stage phyllosoma larvae of scyllarids moulted into the puerulus phase, 9 and 15 days after capture, but both died within 3 days of moulting. Measurements of total body length made before (20·8 mm) and after moulting (13·1 mm) of one of these illustrated the degree of shortening by folding from the phyllosoma phase to the puerulus phase. The puerulus larvae of scyllarids did not appear to feed in captivity, specimens dying 11–25 days after capture not having moulted.

The large numbers of scyllarid phyllosoma larvae taken off the west coast of Australia indicate relatively large breeding stocks about which very little is known.

VII. Discussion

While much of the larval ecology of *P. longipes cygnus* has yet to be studied, these results have enabled more detailed and quantitative studies to be planned with the aim of linking up with concurrent research upon juvenile and adult segments of the population.

The relatively long period of larval development with high but possibly very variable mortality taking place between the time of hatching of larvae and the return of survivors to settle on the coast, has two important applications to studies of the population of *P. longipes cygnus*.

The first is to survey the larvae immediately after hatching in order to estimate the size of the brood stock. This would afford an independent check on the estimate of adult stock based upon detailed statistics of catch and effort obtained from the commerical fishery as used by Bowen and Chittleborough (1966). High catch rates of early phyllosoma larvae taken from inshore waters at night indicate that quantitative sampling might well be used to estimate the size of the brood stock, as has been done by egg and larval surveys for herring (Parrish *et al.* 1959) and pilchard (Southward 1963). In the lobster *Homarus americanus*, Scarratt (1964) found a relation between density of first stage larvae and abundance of parent stock. In the planning of surveys of early larvae care is needed if there are variations from year to year in the time of hatching of eggs, as has been indicated for *P. longipes cygnus* (Section IV(*c*)).

The second important application of studies of larval ecology in this species is to attempt to forecast the strength of a year class by determining the success with which larvae return to settle along the coast. In *Panulirus interruptus*, Johnson (1960) found differences in relative abundance of phyllosoma larvae from year to year during a seven-year study, but he did not relate these apparent variations in year class strength with subsequent abundance as juvenile or adult crayfish. Scarratt (1964) found that the survival of lobster larvae varied from year to year but he could not find a conclusive relation between larvae and the subsequent stock.

This raises the question of the precise age or stage in the life history at which the strength of a year-class is decided. It is generally accepted that in highly fecund fish, larval mortality is very high and subject to wide fluctuations; but actual measurements of survival through this phase (under natural conditions) are very few. Sette (1943) estimated that in the Atlantic mackerel (*Scomber scombrus*) total mortality through the larval phase, over the first 70 days of life, was 99·9996%.

Neither the extent nor the causes of larval mortality in marine crayfish are well understood. As the larvae travel far offshore, one of the causes of mortality could be losses due to adverse current systems. This would act independently of larval density. Crayfish larvae appear to have some ability to maintain position off the same part of the coast despite a prevailing current along that coast (Johnson 1960), but unusual water movements can displace larvae, causing high losses.

Predation is a source of larval mortality which may be density-dependent. From time to time, fishermen off the Australian coast have reported finding phyllosoma larvae in the stomachs of mackerel and tuna. Baisre (1964) has reported 101 phyllosoma larvae of *P. argus* from the stomachs of skipjack (*Katsuwonus pelamis*) and blackfin tuna (*Thunnus atlanticus*) off the coast of Cuba.

While it may not be possible to measure the cause and extent of larval mortality in *P. longipes cygnus*, if the density of late-stage larvae returning to the coast can be measured, fluctuations in survival can be assessed and the strength of the 0-group compared with measurements being made of year classes passing through juvenile age groups. There may be difficulties here in the quantitative sampling of late-stage larvae of this species. Further ecological studies are required, including the diurnal vertical movements of the late phyllosoma phase and the puerulus phase, so that these can be sampled effectively.

The average duration of the phyllosoma phase, approximately 11 months, is much longer than that recorded for other species of marine crayfish, Johnson (1960) recording $7\frac{3}{4}$ months for phyllosoma of *P. interruptus* and Olsen (personal communication) suggesting 4–6 months in the case of *Jasus lalandii*. The prolonged period of larval development in *P. longipes cygnus* might well have a genetic basis, but in addition the phyllosoma larvae spend considerable time far offshore in waters having a very low zooplankton biomass (Tranter 1962) so that food supply might then be limiting the growth rate.

The estimates presented for the wind-generated offshore drift of surface water during summer months are consistent with the observed spread of phyllosoma larvae of *P. longipes cygnus* away from the western coast of Australia. In order to be swept offshore, the early larvae must be close to the surface at least throughout the night, as has been observed. The surface drift induced by the wind extends to a depth proportional to the wind strength. At a depth of 5 m the wind induced current would be approximately one-quarter of that at the surface. Therefore, the precise depth of the maximum concentration of larvae at night is highly important. The surface sampling reported here was mainly in the upper 3 m of the ocean while subsurface sampling was generally taken at depths exceeding 50 m. Future sampling of newly hatched phyllosoma should be taken at small intervals of depth close to the surface in order to find the extent to which these larvae are stratified at the surface at night.

While surface wind drift may play an important role in the offshore movement of early phyllosoma larvae during summer, the method by which late-stage phyllosoma larvae return to the coast is not yet known. The tendency of final-stage phyllosoma larvae not to make diurnal vertical migrations, possibly staying more in subsurface water, may be linked with an onshore movement, but this has not yet been demonstrated.

Those phyllosoma larvae which drift farthest from the coast are no doubt lost, but the maximum distance offshore from which larvae can return successfully is not known. From the sampling which has been carried out so far, it is evident that in late autumn and throughout winter the densities of larvae found within 100 miles of the coast are so low (Table 8) that larvae would need to come in from a greater distance in order to maintain the population.

The phyllosoma larvae of this species apparently cannot return to the coast until the disappearance of the winter wedge of tropical water extending down the coast. In that case it is interesting to speculate on the fate of the larvae in 1956 when the winter low salinity water persisted along the coast through the spring and early summer (Rochford 1969). This could have resulted in the complete failure of that year class to settle on the coast, but no sampling of larvae or juveniles was being carried out at that time.

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STUDIES ON RECRUITMENT IN THE WESTERN AUSTRALIAN ROCK LOBSTER *PANULIRUS LONGIPES CYGNUS* GEORGE: DENSITY AND NATURAL MORTALITY OF JUVENILES

By R. G. CHITTLEBOROUGH*

[*Manuscript received May* 28, 1970]

Summary

Density of juveniles on shallow coastal reefs was measured by a single census mark-recapture method, samples being taken by baited traps. Verification that marked and unmarked individuals were equally vulnerable to trapping was obtained by double marking and direct underwater checking. Very little dispersal or migration of the juveniles occurred from January to October, but in November and December the larger specimens moved to deeper water while smaller juveniles (age group 2+ years) appeared on the reefs by January. In a test area away from the centre of the coastal range of this species, density of juveniles at the beginning of each of the past five years fluctuated greatly from one year to another (ranging from 5385 per ha in January 1967, to 1212 per ha in January 1969). Natural mortality of juveniles varied with density ($M = 0{\cdot}499D_0 \times 10^{-3}$), shelter possibly limiting the carrying capacity of a reef. In aquaria, cannibalism of newly moulted rock lobsters has been shown to increase with crowding, despite surplus feeding.

Density-independent factors operating upon planktonic larvae and density-dependent factors limiting survival of juveniles play complementary roles in determining the level of recruitment to the adult stock. In the centre of the population range, the second set of factors is of major importance; towards the periphery of the range, the first set of factors is the more important.

Catchability declined with water temperature in autumn and increased in spring. In January of five successive years (temperature 22·2–23·2°C) catch per unit effort was directly proportional to population density ($c/g = 5{\cdot}05D \times 10^{-3}$). However, catchability rose from $2{\cdot}5 \times 10^{-3}$ in January 1966 to $15{\cdot}8 \times 10^{-3}$ in January 1969, possibly due to a decline in the availability of natural food.

I. INTRODUCTION

P. longipes cygnus George is confined to the western coast of Australia, from Northwest Cape to Cape Naturaliste (Fig. 1). The majority of the commercial catch is taken between 28°S. and 32°S. (Sheard 1962). The juveniles are concentrated mainly on shallow coastal limestone reefs (to depths of 9 m or 5 fm, with some larger juveniles to 18 m or 10 fm), while the adults are generally confined to deeper waters (27–155 m, or 15–85 fm). During the prolonged larval phase, the planktonic larvae are carried some hundreds of miles from the coast (Chittleborough and Thomas 1969).

Chittleborough and Thomas suggested that the strength of a year class is dependent initially upon the effectiveness of ocean currents in returning the final-stage larvae to the coast. However, as yet, a quantitative method of measuring settlement along the coast (towards the end of the first year of life) has not been devised.

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Juveniles from age group 2+ years are concentrated on shallow coastal reefs and enter baited traps readily, so that the density can be measured by mark and recapture techniques, provided that certain assumptions are satisfied. In this paper a method of measuring the density of these juveniles is described, and changes in density and natural mortality within an area of natural reefs are followed over successive years. These results, supplemented by data from other points along the coast, give some insight into the factors controlling recruitment in this population. Data upon growth will be presented in a later paper.

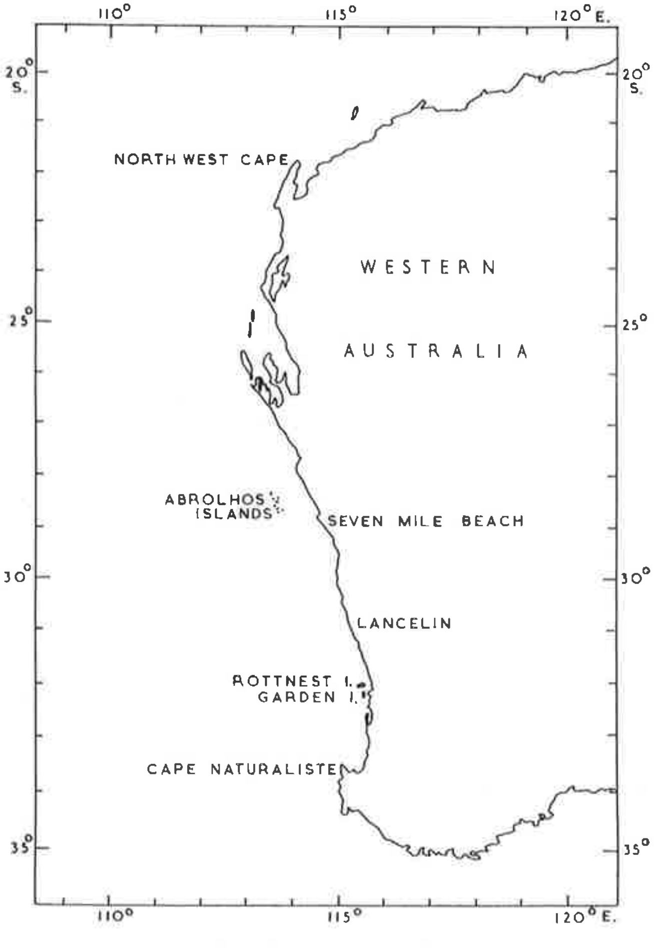

Fig. 1.—Locations mentioned in the text.

Most of the research was sited on the western side of Garden Island (Fig. 1) in an area 2 km long and extending 400 m from the shore, closed to both amateur and commercial fishing. In this area a series of limestone reef platforms, similar in structure and in plant and animal communities to the reef platforms at nearby Rottnest Island (described by Hodgkin, Marsh, and Smith 1959; Phillips 1969) extended from the shore. Other reefs, 50–250 m off the coastal platform, dampened the force of wave action, which can be severe on the exposed side of this island. Three separate sections of reef (0·2–0·5 ha in area) in water up to 5 m deep, were selected for intensive study.

Some sampling was also carried out at Lancelin and at Seven Mile Beach (Fig. 1), on reefs of similar structure and depth to those in the main test area at Garden Island.

On each of these shallow coastal reefs, all the rock lobsters were sexually immature.

II. Measurement of Population Density

A single census method was used to measure the density of pre-recruits on each section of reef. Marking was carried out for several successive days, the population then being left undisturbed for at least three weeks before trapping again in the recapture phase. The traps were of rectangular "parlour-and-bedroom" design (collapsible for ease of transport in small boats as used by De Bruin (1960)). For uniformity, fish heads or whole fish were used as bait, stale fish being discarded as this is less attractive to rock lobsters (Fielder 1965). To maximize the catch, each trap was set in a hole or under a rock ledge by a diver.

After one night, the traps were raised and each rock lobster was sexed, measured, and marked, then released at the point of capture. Marking was either by the clipping of a pleopod, cutting one of the lateral spines on the abdomen, or by punching a hole 3 mm in diameter into telson or uropods. Animals from adjacent reefs were marked distinctively so that dispersal from one reef to another could be checked.

Because fishermen have observed that catchability is depressed at times of full moon, trapping for marking and recapture was carried out round the time of new moon to maintain a large sample size.

Various formulae, reviewed by Jones (1964), were applied to estimate numbers present in each reef. Similar results were obtained from the formulae, as a high proportion of the population of each reef was marked and recaptured. Because weather conditions often restricted work at sea, direct sampling was used rather than inverse, i.e. sampling was continued until a predetermined sample size was obtained, rather than until a predetermined number of marked rock lobsters had been recaptured. The estimate used for the population size ($\hat{N}$) and its variance was that of Bailey (1951), i.e.

$$\hat{N} = \frac{T(n+1)}{m+1} \qquad \mathrm{var}(\hat{N}) = \frac{T^2(n+1)(n-m)}{(m+1)^2(m+2)},$$

where T is the total number marked and m is the number of marked individuals in a subsequent sample of n rock lobsters.

The reliability of the population estimates depends on the following assumptions:

(i) That the marked individuals are distributed at random throughout the population on that reef;

(ii) that the marking itself does not increase mortality significantly;

(iii) that all marked individuals recaptured are recognized and reported;

(iv) that marked and unmarked individuals are equally likely to be captured during the second (recapture) phase of each experiment;

(v) that dispersal and migration are not taking place during the interval between marking and recapture.

Each of these assumptions will now be examined.

(i) *Random Distribution of Marked Individuals Within Each Reef Population.*—By re-setting traps progressively across the reef each day and releasing at the point of capture, marked individuals were distributed across that reef. In the period before the first recapture phase of each experiment, further intermingling of marked and unmarked rock lobsters occurred during nightly foraging so that, when trapping was recommenced, the marked specimens appeared to have been well dispersed through the population upon that reef.

(ii) *Marking Mortality.*—Each of the methods of marking was tested in aquaria against unmarked controls and had no effect upon subsequent survival or growth of juvenile rock lobsters. Rock lobsters released above a reef generally regained shelter without further losses. Although they were removed from the water only for a short time for measuring and marking, and quite active when released, some were slow to seek complete shelter within the reef. Rock lobsters could be observed easily when released onto these very shallow reefs and only once was one seen to be taken by a predator (an octopus).

(iii) *Incomplete Reporting.*—This was not a problem as recoveries were obtained from our own trapping in an area closed to commercial or amateur fishing. Marks could be distinguished after several successive moults, the scar tissue being distinctive even if the appendage had regenerated completely.

(iv) *Marked and Unmarked Equally Liable to Capture.*—This is a most important pre-requisite to any population estimate. In order to test this assumption, a double-marking experiment was carried out on an isolated reef which had limited cover, so that many of the rock lobsters could be checked visually underwater. A small reef in shallow water (4 m) at Lancelin was selected for this purpose. As well as the clipping of a pleopod, rock lobsters were marked across the carapace with an epoxy-resin paint which was clearly visible to divers during underwater inspection. The epoxy resin was highly effective as it could be applied to the wet surface of the carapace (even applied underwater), hardening after the rock lobster was released and having good adhesion to the spiny surface. Some specimens held in aquaria until moulting showed no adverse effects from marking with epoxy resin.

In this experiment, 198 juvenile rock lobsters were double-marked during two successive nights of trapping. One week later, an underwater check was made by two divers who counted the more exposed individuals, recording those which carried the epoxy resin. Traps were then set and the proportion of marked individuals were recorded in the catches for the next two nights. The rock lobsters were released on the reef immediately after examination. The operation of direct underwater check followed by trapping was repeated four weeks after the original marking had been carried out. By that time, 36·8% of the double-marked rock lobsters recaptured in the traps had moulted, discarding the epoxy resin. The proportion of marked rock lobsters seen underwater at that time was adjusted to allow for this loss by moulting.

The estimates of population size obtained from these data (Table 1) show that one week after marking, the marked individuals are more likely to enter baited traps than unmarked specimens, resulting in the population size being underestimated. However, trap returns four weeks after marking gave results consistent with those obtained by the more direct (but more difficult) method of underwater observation. Therefore, in the single census method involving marking at the time of new moon, followed by retrapping at the next period of new moon, sampling from the marked and unmarked populations is equally likely during the second period.

TABLE 1

ESTIMATES OF ROCK LOBSTER POPULATION ON ISOLATED REEF USING DOUBLE MARKED INDIVIDUALS

Total of 198 double-marked initially. Subsequent results from visual examination underwater (marked with epoxy resin) compared with recaptures by baited traps (marked by clipping a pleopod)

Interval after Marking	Underwater Examination				Results from Trapping			
	Number Examined	Marked No.	Marked %	Estimated Population	Total Catch	Marked No.	Marked %	Estimated Population
1 week	146	23	15·8	1213±446	129	38	29·5	660±171
4 weeks	160	22*	13·8	1386±524	221	38	17·9	1127±324

* After adjustment for loss of epoxy resin by moulting.

(v) *Dispersal and Migration.*—Ideally, the population on a particular reef should be a closed one for the period within which a single census estimate of population size is being made.

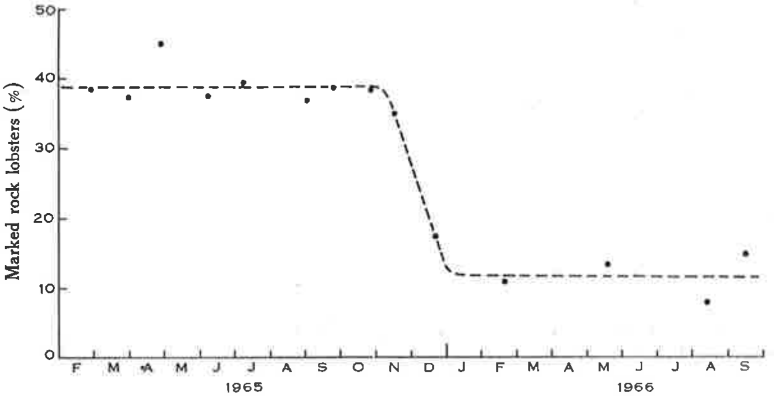

Fig. 2.—Percentage of marked rock lobsters in catches from Reef A after marking 1611 in January 1965.

Rock lobsters taken at the same time from several adjacent reefs were of almost identical size composition so that any interchange during normal foraging movements could not be distinguished by changes in size distribution. If there was random interchange between adjacent reefs, the marking of a large number on one reef would be followed by the appearance of increasing numbers of these marked individuals on adjacent reefs and a progressive diminution in the percentage of marked rock lobsters remaining in the population on the original reef. However, in practice it was found that there was very little movement of marked rock lobsters from one reef to another. After marking in a reef population during January, the percentage of marked rock lobsters in subsequent catches each month from that reef remained almost constant until the following October (Fig. 2), showing that there was negligible dispersal from one reef to another during that time. During November and December the percentage of marked individuals in the reef population declined abruptly, indicating that the population was not closed at that time of the year.

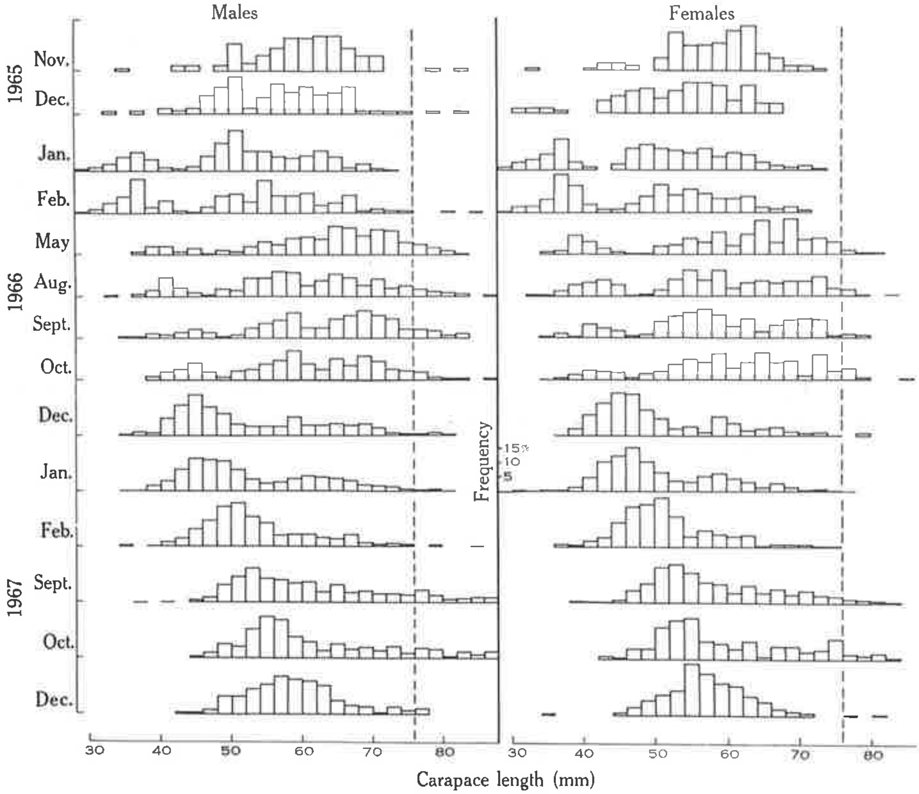

Fig. 3.—Length frequency distribution of male and female rock lobsters in the Garden Island test area from November 1965, to December 1967.

Figure 3 shows that within the test area at Garden Island there was an influx in January 1966, of small juveniles into the catches. These small juveniles, having a modal carapace length of 36–37 mm, are considered to be the 2+ age group. During succeeding months, growth of the various age groups of rock lobsters was reflected in a progressive shift to the right of the various modal size groups. In October, just before the spring moult, a considerable proportion of the males and females was approaching the legal minimum size (carapace 3 in. or 76 mm).

Figure 3 shows an abrupt change in the composition of the population in December 1966. The larger males and females disappeared from the shallow reefs, while the 2+ age group (modal size now 45 mm) had become fully vulnerable to trapping. By October 1967, a further portion of the males and females had grown to near legal size, and in December 1967, these larger rock lobsters had disappeared from the test area.

Each year, the disappearance of the larger juveniles from the shallow reefs coincides with a sharp increase in catch rate at the beginning of December by fishermen operating just outside the coastal reefs. These commercial catches consist of pale newly moulted immature rock lobsters. Examination of fishermen's catches taken close to the test area resulted in the recapture of some of the larger specimens previously marked on the test reefs.

TABLE 2

DENSITY (NUMBER PER HECTARE) AND MORTALITY COEFFICIENTS OF JUVENILE P. LONGIPES CYGNUS WITHIN GARDEN ISLAND TEST AREA, 1965–1969

Year	Reef	Initial Density				Density in Spring		Mortality Coeff. M_t	Time (weeks) t	Mortality/ Week $(10^2 M)$
		Date	Total Stock	Recruits	Residual Stock	Date	Total Stock			
1965	A	Jan. 19	5144±237	*	*	Sept. 2	2352±252	0·782	32	2·44
1966	B	Jan. 20	2834±304	1947	887	Aug. 17	2305±304	0·206	30	0·69
1967	AC	Jan. 7	5421±445	4225	1196	Sept. 7	1811±282	1·095	35	3·13
	B	Jan. 7	5350±445	3425	1925	Sept. 7	2167±284	0·903	35	2·58
1968	A	Jan. 25	1465±173	516	949	Sept. 19	1159±203	0·234	34	0·69
	B	Jan. 25	1947±143	277	1670	Sept. 19	1403±190	0·327	34	0·96
	C	Jan. 25	1846±247	272	1574	Sept. 19	1025±190	0·586	34	1·72
1969	A	Jan. 19	1460±156	660	800	Aug. 17	912±195	0·471	30	1·24
	B	Jan. 19	1433±106	272	1161	Aug. 17	1342±222	0·066	30	0·22
	C	Jan. 19	1137±104	88	1049	Aug. 17	1119±168	0·016	30	0·05

* Not possible to separate new recruits from residual stock.

Thus the population of immature rock lobsters on the shallow coastal reefs is static on each reef from January to October, followed by emigration of the larger (older) individuals towards deeper water in November and December. As the larger rock lobsters move out, younger ones (3+ age group) become more vulnerable to trapping, and very young rock lobsters (2+ age group) are recruited on to the reefs.

Most of the pre-requisites for reliable estimate of population size using the single census method are thus fulfilled if the mark-recapture data are gathered as described during the first 10 months of each calendar year.

III. DENSITIES RECORDED ON TEST REEFS

Estimates of population size were made on one or several adjacent reefs in the test area at Garden Island at the beginning of each year and again during the following spring, before emigration occurred. At any one time the populations of adjacent reefs were of similar density (Table 2) and size composition. From the carry-over of marked individuals from one year to the next, it was possible to distinguish at the beginning of each year the segment of the population remaining for the second successive year from those which had just been recruited.

Table 2 shows that the initial population density varied widely from year to year, due to considerable variations in recruitment. When these initial densities are considered in terms of size distribution (Fig. 4), a clearer picture of the success of various year classes begins to emerge. The group of small juveniles (modal length 36 mm) which appeared on the reefs at the beginning of 1966 were of the 2+ age group and hence were representatives of the crop of larvae hatched in the spring and summer of 1963–64. This year class of 1963–64 appeared in the catches in January 1966, but at that time was not as vulnerable as older age groups, since the density of this year class apparently increased in January 1967 (Fig. 4). This highly successful year class was present in the test area for four successive years, the modes shown in Figure 4 being linked by progressive shifts evident in catches made at short intervals during each year (as illustrated in Fig. 3) and also by the growth of marked individuals.

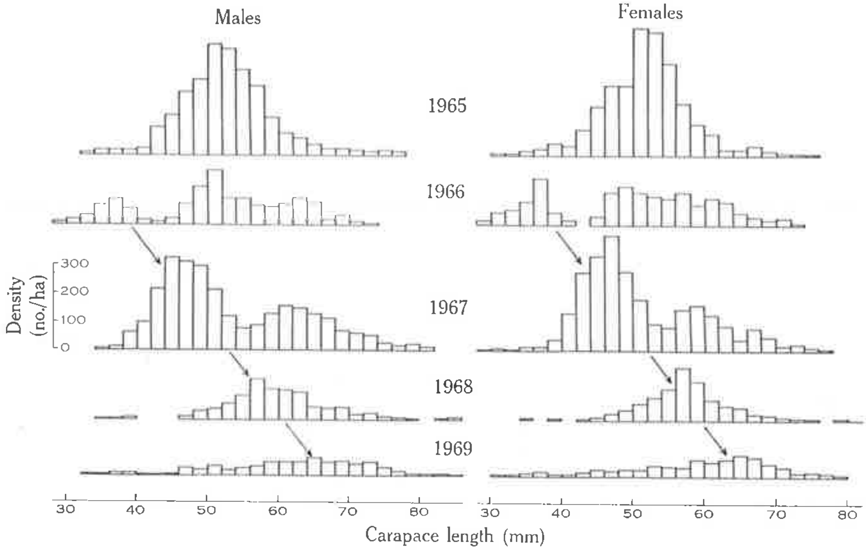

Fig. 4.—Density and size composition of rock lobster population in the Garden Island test area during January of each year from 1965 to 1969.

Figure 4 shows that in each of the three years since the first appearance of the successful 1963–64 year class, subsequent year classes have been poorly represented in the catches. The population structure in January 1969 shows only low numbers of the 2+ and 3+ age groups. Even allowing for the possibility that the 2+ age group may be slightly under-represented in these estimates, there can be no doubt that very few of the members of the year classes of 1964–65, 1965–66, and 1966–67 survived through larval and early postlarval life in this locality.

IV. Natural Mortality of Juveniles

As the population on a reef is virtually closed to migration and dispersal between January and October, and as the test area is not open to fishing, any decrease in density during that period will be due to natural mortality. The coefficient of natural mortality for that period (M_t) can then be determined from the change in density with time, i.e.

$$\frac{D_t}{D_0} = \exp(-M_t).$$

Table 2 shows that the natural mortality coefficient (M) is highest during years when the initial density is greatest. In fact, there may be a direct relation between initial density (D_0) in a particular year and subsequent mortality (M) during that year, the regression, shown in Figure 5, being

$$M = 0\cdot 499 D_0 \times 10^{-3}.$$

The standard error of the regression coefficient is $0\cdot 047 \times 10^{-3}$. This regression accounted for 92·6% of the variation about the origin.

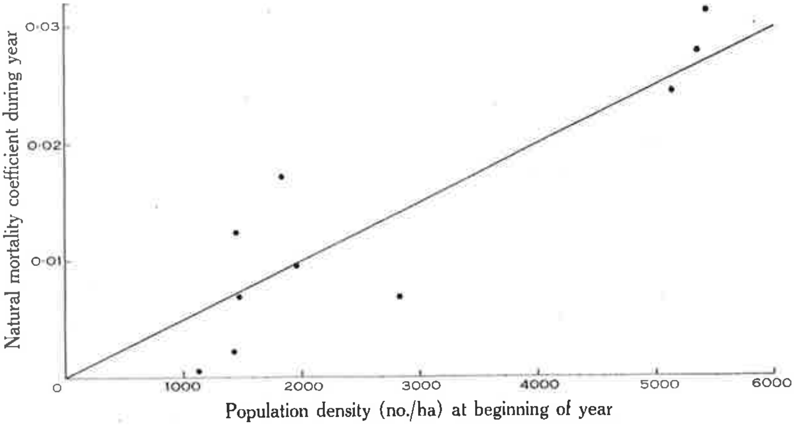

Fig. 5.—Relation between natural mortality coefficient (per week) during a year to population density at the beginning of that year.

One explanation of the apparently high mortality during years of high initial population density might be that in such years there is premature emigration of larger individuals (4+ and 5+ age groups) to deeper waters, resulting in an unduly high estimate of natural mortality. The movements of marked rock lobsters did not support this hypothesis. A further check was possible using the data from the test area in 1967, where the 3+ age group could be separated from the older juveniles. In January of that year, the 3+ age group was at a density of 3514 per ha, while at the beginning of October (35 weeks later) the density of this age group was 1300 per ha. Then,

$$\frac{1300}{3514} = \exp(-M_t) \text{ and } M = 0\cdot 028.$$

This is almost identical with the estimates of the natural mortality coefficient for the total population present in the test area during 1967 (0·026 and 0·031, see Table 2), supporting the original conclusion that natural mortality on these reefs is being determined by a density-dependent factor.

The density of the survivors on the test reefs in the spring was almost the same in 1965, 1966, and 1967, irrespective of the initial density at the beginning of these years. Thus the carrying capacity of these reefs may be limited to a density well below that at which they are sometimes seeded with post-larvae of successful year classes.

Juvenile rock lobsters held in aquaria under crowded conditions (groups of five with 450 cm^2 floor area each, or groups of 16 with 250 cm^2 floor area each) tended to moult more frequently than individuals of the same age group held in isolation (900 cm^2 or 4000 cm^2 floor area) as shown in Figure 6. However, under crowded conditions the newly moulted rock lobsters were often killed by their fellows, despite the availability of excess food. Mortality associated with crowding occurred irrespective of whether age groups were mixed or members of only one age group were present. Under less crowded conditions an animal about to moult can move away from the rest of the group so that this type of mortality did not occur. These observations afford a possible explanation of the relation between natural mortality and population density on the coastal reefs.

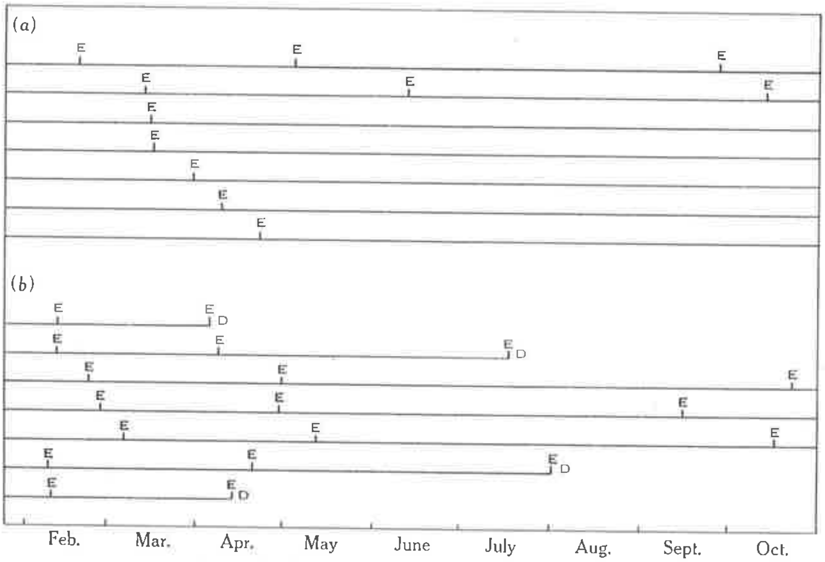

Fig. 6.—Times of ecdysis (E) and death (D) of individual rock lobsters aged 2+ yr held in aquaria during 1969, (*a*) singly and (*b*) crowded together; all supplied with excess food.

V. Emigrants to Fishing Grounds

Because both emigration and immigration are occurring during November and December, it is not possible to estimate population density on the reefs of the test area in that period, nor to measure directly the quantity of rock lobsters moving out into the adjacent fishing grounds. Some index of the potential level of emigration from the test area can be obtained from the size and composition of the population present in September or October, if the sizes of emigrants are known. This can be obtained from the examination of fishermen's catches taken at depths of 7–14 m just outside the test area late in November and early in December. At that time the fishermen's catches consist of pale-shelled, newly moulted juveniles, locally called "white" rock lobsters (George 1958), together with some normal coloured "red" rock lobsters which are generally smaller than the "whites". Figure 7 shows that the size range of the "white" rock lobsters taken just outside the test area corresponds to that part of the population disappearing from the test area between October and December. The smaller "red" rock lobsters in fishermen's catches were mainly from the resident stock on those grounds. Careful examination of the rock lobsters taken by fishermen at this time resulted in the recovery of some which had been marked previously in the test area.

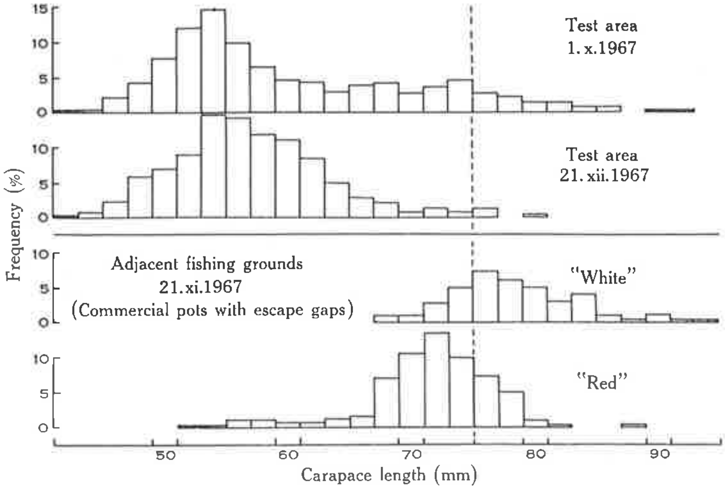

Fig. 7.—Size composition of rock lobsters in Garden Island test area (0–4 m) in October and December 1967, compared with catch by fishermen's pots (escape gap fitted) on adjacent fishing grounds (7–14 m) in November. Minimum legal length (76 mm) – – – –.

Although fishermen's traps are fitted with escape gaps (by regulation), the "white" rock lobsters are fully sampled as shown by Figure 7, smaller "red" rock lobsters also being captured (and subsequently rejected from the commercial catch).

Because of annual fluctuations in growth rates, the size composition of "white" rock lobsters varies from year to year (Table 3). The annual variations in mean length are consistent in both sexes. By subtracting 5 mm (approximately two standard deviations of the mean), a lower limit of size is obtained for the emigrants of each sex. In each case, the value derived in this way from Table 3 corresponds to the size of rock lobsters which have left the test area by December (Fig. 3). A further 5 mm subtracted from this length yields the lower limit of the size of potential emigrants in September immediately before the spring moult, since marked individuals of this size range gained a mean of 5 mm in carapace length per moult.

By applying lengths derived in this way to the density and size composition of the population present in the test area in September, an estimate of the potential level of emigration from the shallow coastal reefs at the end of each year is obtained (Table 4). While the level of emigration to the fishing grounds has varied to some extent from year to year, Table 4 shows that wider variations in recruitment to the fishable stock have occurred owing to differences from year to year in the proportion of the emigrants which have attained the legal size. In some years (e.g. 1967 and 1969)

Table 3

"WHITE" ROCK LOBSTERS SAMPLED FROM FISHING GROUNDS ADJACENT TO GARDEN ISLAND TEST AREA IN LATE NOVEMBER AND EARLY DECEMBER AT DEPTH OF 7–16 m

Carapace Length (mm)	Males					Females				
	1965	1966	1967	1968	1969	1965	1966	1967	1968	1969
<64				1						
64									1	
65	1					1			1	
66	1					1			1	1
67				1		5	2		4	1
68	1			2		7	2	2	9	1
69	3			3		4	11	3	19	3
70	3	2	1	5	1	3	7	2	40	2
71	1	3		8	1	2	11	2	23	11
72	4	5	1	13		4	16	5	41	12
73	2	12	3	14	5	1	21	5	33	16
74	3	21	4	18	3	3	14	8	24	25
75	1	7	5	17	10	2	27	9	30	26
76*	1	25	9	8	11	5	18	11	19	31
77	1	14	7	21	10	1	11	11	13	18
78		20	9	16	20		10	6	8	26
79	1	9	12	11	16	3	12	5	9	20
80	2	13	6	11	28	3	4	12	9	14
81	1	14	9	7	14	1	1	4	4	11
82		13	1	5	10	1	5	4	3	11
83	1	10	7	5	19	1	3	4	2	5
84		5	7		10	1	1	5		4
85	1	6	4	4	9	1	2	5		3
86	3	1	2		2		2			2
87		3	2		9			1		2
88		5		1	3					3
89	1		1		4					
90			4	1	4			1		1
91	1		1		1					1
92			1							
93					1					
94			1		1					
Total	33	188	97	172	192	50	180	105	293	250
Mean Length	76	78	80	76	81	73	75	77	73	77

* Minimum length for commercial catch.

the majority of the emigrants from shallow coastal reefs are of legal size and are exposed immediately to fishing pressure at the opening of the fishing season, while in other years (especially 1965) few of the emigrants are vulnerable, requiring at least one or even two further moults before reaching the legal minimum size.

In theory, the estimates derived from the test area at Garden Island for the annual levels of recruitment to the fishable stock, should bear a direct relation to the catch rates achieved by fishermen operating close to the test area at the opening of the fishing season. Two problems have been encountered here. On the one hand, there were not sufficiently detailed data upon commercial fishing operations (this is being rectified), and on the other hand, the question arises as to whether the fishable stock was equally vulnerable to the fishing gear (baited traps) in each year, i.e. whether "catchability" was constant.

TABLE 4

DENSITY OF POTENTIAL EMIGRANTS FROM GARDEN ISLAND TEST AREA AT END OF EACH YEAR AND PROPORTION OF THESE WHICH WILL HAVE ATTAINED LEGAL SIZE AT OPENING OF FISHING SEASON

Year	Density of Potential Emigrants (No./ha)		Per cent of Emigrants Fishable
	Total	Legal Size in Nov.–Dec.	
1965	504	99	19·6
1966	756	413	54·6
1967	400	299	74·7
1968	586	230	39·2
1969	502	388	77·3

VI. CATCHABILITY: THE RELATION BETWEEN DENSITY AND CATCH PER UNIT EFFORT

In the analysis of catch statistics from commercial fisheries, one of the basic assumptions has been that catch per unit effort is directly proportional to population density (Ricker 1940; Gulland 1964; Bowen and Chittleborough 1966), i.e.

$$c/f = qD.$$

The constant q, the catchability coefficient, is then the proportion of those fish present within unit area which is captured by the operation of one unit of effort.

On fishing grounds it is rarely possible to test this assumption since the actual density is not known. However, within the test area at Garden Island the mean catch per unit effort was measured independently at the same time as each estimate of density was made.

The pattern shown in Figure 8 for 1965 was typical of the seasonal changes recorded in several successive years. During the year there is a relation between catch per unit effort and population density upon that reef system, but factors other than availability of rock lobsters (density) are causing variations in catch per unit effort. Catchability is slightly depressed during January but relatively high in February and March. This is consistent with reef and aquarium observations that considerable numbers of juveniles moult during January, and are less vulnerable to capture. Food intake is highest immediately after moulting, increasing the probability of capture by baited traps.

From April to June, the catch per unit effort fell rather steeply, catchability apparently declining with water temperature, as shown by McLeese and Wilder (1958) for the lobster *Homarus americanus* Milne Edwards. With increasing temperatures in the spring, catchability rose considerably (Fig. 8). If there had been no precise evidence of population density and structure, the increase in catch per unit effort recorded from July to October might have been wrongly interpreted as indicating immigration into the shallow coastal reefs early in the spring.

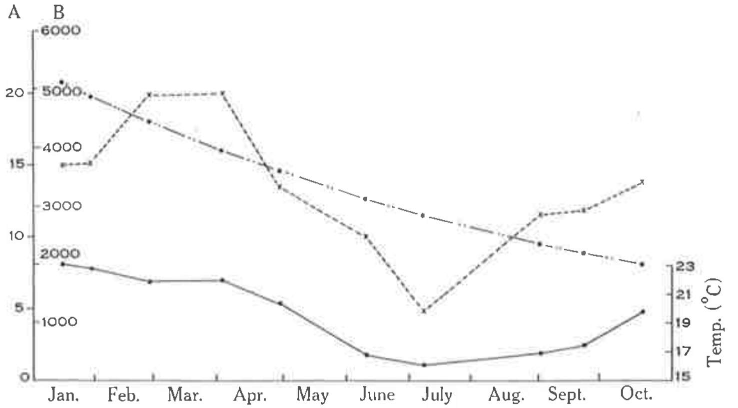

Fig. 8.—Changes in population density (no./ha) (●— · · —●) (B), catch per unit effort (no./trap-night) (×– – – –×) (A), and water temperature (● —— ●) on reefs of Garden Island test area during 1965.

To determine the relation between catch per unit effort and population density without the added complication of temperature-induced variation in catchability, data obtained from the test area in January of each of the past five years have been examined. Mean water temperatures in this month did not differ significantly from one year to another, ranging from 23·2°C in January 1967, to 22·2°C in January 1969. The regression coefficient (regression through the origin) with its standard error, for the data shown in Figure 9, is $5\cdot05\times10^{-3}$ ($0\cdot521\times10^{-3}$). The regression was highly significant ($P < 0\cdot001$), accounting for 71·2% of the variation about the origin. The regression coefficient provides a measure of the mean catchability coefficient (q) for unit area (one hectare) during January of those years. However, estimates of q for January of individual years (Table 5) varied considerably. Catchability was at a similar low level in 1965 and 1966 (although population density differed greatly in those two years); then from 1967 to 1969 catchability increased greatly.

Some other factor not related directly to population density or to water temperature at the time of fishing is apparently affecting catchability. Since catches are taken by baited traps, this factor might operate through feeding behaviour. If the rock lobsters were "hungrier" in one year than another, they would be more likely to enter baited traps, i.e. catchability would increase. This implies that the food available to the rock lobsters on these reefs is limited at times, either due to a direct decline in food material present, or by increased competition (from other species) for the same food. So far it has not been possible to check either of these hypotheses.

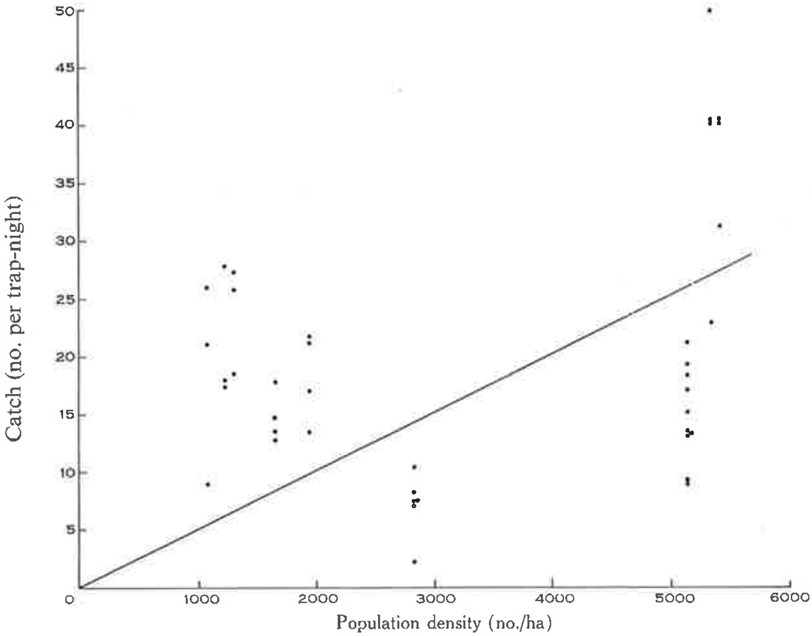

Fig. 9.—Catch per unit effort and population density recorded on reefs in Garden Island test area during January of each year from 1965 to 1969.

TABLE 5

MEAN CATCH PER UNIT EFFORT, POPULATION DENSITY, AND CATCHABILITY OF ROCK LOBSTERS ON REEFS IN GARDEN ISLAND TEST AREA DURING JANUARY OF EACH YEAR 1965–1969

Year	Reef	Mean Catch per Trap-Night (n)	Density (No./ha) (D)	Catchability Coefficient $n/D = q(\times 10^2)$
1965	A	14·93	5145	0·29
1966	B	7·14	2834	0·25
1967	AC	37·11	5421	0·68
	B	37·68	5350	0·70
1968	AC	14·96	1656	0·90
	B	18·63	1947	0·96
1969	A	21·07	1460	1·44
	B	24·90	1433	1·74
	C	18·69	1137	1·64

VII. Sampling in Other Areas

The same gear was used to examine juvenile rock lobsters present on shallow coastal reefs at other localities along the western coast of Australia but sampling was less regular and no marking was carried out for estimates of density.

In general, catch rates indicated an increase in mean density of juveniles as one moved north from Garden Island towards the centre of the north–south geographic range of this species. At Seven Mile Beach (29°08′S., 114°53′E.), close to the centre of the range, catch rates were relatively high and less variable than at Garden Island during corresponding months (Table 6). Unfortunately, samples were not taken at Seven Mile Beach at the beginning of 1967 when the catch rate and population density at Garden Island were maximal (Table 2). Although catchability has been shown to vary from month to month at a particular locality and may also differ between localities at the same period of time, Table 6 indicates that population density on reefs at Seven Mile Beach is at a higher mean level than at Garden Island and less subject to oscillations from one year to another. This may indicate that settlement of larvae in the centre of the coastal range varies around a higher mean level than on the part of the coast nearer to the periphery of the population. Confirmation of this has been obtained by Phillips (personal communication).

Table 6

CATCH PER UNIT EFFORT FOR JUVENILES IN TWO SIMILAR HABITATS

Mean number of rock lobsters per trap per night recorded near the centre of range (Seven Mile Beach, 29°10′S.), and towards the periphery (Garden Island, 32°10′S.)

Month	Garden Island	Seven Mile Beach
Nov. 1965	9·7	40·5
Jan. 1967	39·1	no sample
Feb. 1968	14·7	35·9
Oct. 1968	13·4	34·6
Feb. 1969	12·7	38·8

The structure of the juvenile population present on shallow reefs at Seven Mile Beach was similar to that at Garden Island. The same size (age) groups were present and there appeared to be some fluctuations in year class strength, though not of the same magnitude as at Garden Island. The pattern of emigration of larger individuals towards the end of the year, followed by the appearance of small juveniles (age groups 2+ and 3+ years), also occurred at Seven Mile Beach, but there were indications that this occurred slightly earlier than at Garden Island which is nearly 370 km (200 nautical miles) to the south.

VIII. Discussion

Much remains to be clarified before a comprehensive picture can be presented of the oscillations in success of individual year classes of rock lobsters through the juvenile phase, and of the limiting factors involved. In particular, more data are needed from the centre of the north–south range of the population (e.g. in the vicinity of Seven Mile Beach). However, from the data presented, an outline can be given of the probable sequence of events through the pre-recruit phase in this species.

Settlement of final stage larvae (the puerulus stage) along the coast fluctuates very greatly in abundance from year to year, apparently as a result of density-independent factors such as current systems operating upon the planktonic larvae, as suggested by Chittleborough and Thomas (1969). Settlement in the centre of the coastal range varies around a higher mean level than on that part of the coast which is nearer the periphery of the population.

The holding capacity of the coastal reefs in which the post-larvae spend several years as juveniles is limited by the shelter (and possibly food) available. The limitations of shelter introduce a density-dependent factor restricting the survival of juveniles. At moderate levels of density, juveniles tend to aggregate together under a ledge with few or none in adjacent shelter. In that situation, an individual in pre-moult can leave the group and moult in the isolation of an adjacent shelter. But at high levels of density, there will be other aggregations of juveniles in the nearby shelter so that moulting animals must either stay with others and risk attack by members of the same species (which occurs even when food supply is not restricted), or moult away from shelter, being exposed to predation by other species.

Although the holding capacities of the various reefs have not been measured, the coastal reefs near the centre of the rock lobster population are of similar structure and contain similar flora and fauna to the reefs located towards the southern part of the range, so that for present purposes the reefs from the various sections of this coastline will be assumed to afford similar resources (food and shelter). If the holding capacity of reefs was determined mainly by the amount of shelter afforded, rather than variations in food material available, then the holding capacity of a particular reef would tend to be constant from one year to another. However, from the evidence presented in Section VI, the possibility of long-term changes in availability of food warrants further investigation.

At the centre of the population, settlement of postlarvae, though highly variable, is generally in excess of the holding capacity of the coastal reefs so that density-dependent mortality of juveniles limits recruitment to the adult stock (in deeper water) to much the same level each year.

On the other hand, towards the periphery of the population, settlement of postlarvae is seldom in excess of the holding capacity of the coastal reefs, so that density-dependent mortality becomes effective only when a year class has been particularly successful in settling in that region. Recruitment out to the adult stock would then reflect the fluctuations of year classes produced by the density-independent factors operating on larvae, dampened to some extent by density-dependent factors removing excess juveniles in certain years. The mean level of recruitment to the adult stock would thus be lower in the periphery than at the centre of the population.

These two separate controls (density-independent mortality of larvae, and density-dependent mortality of juveniles) are then complementary. When the former is only mildly effective, so that a large crop of postlarvae settle on the coastal reefs, the latter becomes effective in limiting the level of recruitment. Since neither of these controls is operating upon the adult section of the population, the level of recruitment must be independent of the size of the brood stock, at least over a wide range of adult stock size.

From this model, the prospects for raising the level of recruitment by direct intervention can be explored. In theory, seeding the coastal reefs away from the centre of the population, with puerulus larvae or early postlarvae, would increase the level of recruitment, as in most years the natural settlement of larvae is below the holding capacity of the reefs. On the other hand, seeding of reefs near the centre of the population would almost always be wasteful because natural settlement of larvae is usually more than adequate. The question of seeding reefs is largely academic at present, since the prospects for mass culture through the long larval life are poor in this species.

A more practical approach to raising the level of recruitment might be to distribute artificial shelters along the coast. In the centre of the population range, an artificial increase in the holding capacity of coastal reefs would be likely to reduce the wastage of postlarvae and so increase recruitment in most years. On the other hand, erection of artificial reefs along the coast towards the periphery of the population would generally be ineffective in aiding recruitment.

Trials of artificial shelters are now being carried out at various points along the coast.

IX. ACKNOWLEDGMENTS

I am grateful to the Minister for Fisheries and Fauna, for closing the test area at Garden Island to commercial and amateur crayfishermen, and to N. A. Campbell (Division of Mathematical Statistics, CSIRO) for assistance and advice in the treatment of data.

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Paper 18

COMMONWEALTH SCIENTIFIC AND INDUSTRIAL RESEARCH ORGANIZATION

DIVISION of FISHERIES and OCEANOGRAPHY

Report No. 56

DEVELOPMENT OF A TAG FOR THE WESTERN ROCK LOBSTER

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Summary

Several types of tags were tested on the western rock lobster *Panulirus longipes cygnus* George, seeking a multi-purpose tag having high retention through successive moults, low mortality due to tag, and no inhibition of either growth or mobility.

The Western Rock Lobster Tag was developed by combining the most suitable features of the Gundersen Tag and the Sphyrion Tag. Field trials have shown that this tag fulfilled most of the requirements although tag mutilation (owing to gregarious behaviour of this species) has not been eliminated entirely.

INTRODUCTION

Marking or tagging of crustacea which undergo regular ecdyses presents problems. Tests leading to the development of a multi-purpose tag, highly effective for the western rock lobster, *Panulirus longipes cygnus* George, are described here. It should be noted that a method satisfactory for one species may be less effective for even a closely related species, due to slight differences in anatomy, behaviour, or habitat.

For short-term identification of individual rock lobsters held in aquaria, numbers painted on the carapace with epoxy-resin ("Vepox" trowelling resin) have been used. This epoxy-resin is effective as it can be applied to damp surfaces, adheres well to the rough spiny shell of this species, and hardens underwater so that the rock lobsters can be returned to their tanks immediately after marking. The mark can be re-applied to the new shell a few days after each moult (at the time of measuring for growth studies).

In the field, considerable use has been made of tail punching or clipping appendages (Chittleborough 1970). This is effective when dispersion is minimal and the research team relies on its own efforts to recapture (and identify) marked individuals. A coded series of small holes punched into telson and uropods recorded the carapace length (to the nearest millimetre) at that time, while the clipping of a particular abdominal spine or pleopod identified the time of marking. Such specimens were useful both for short-term growth studies (up to one year) and also for mark-recapture estimates of population density. Even when the holes in the telson or uropods were healed after two or three moults, the scars could still be recognized through several more moults.

Clipping or punching has limited uses since individuals cannot be distinguished and fishermen cannot be expected to recognize such marks. A tag carrying its own serial number is needed for long-term studies, especially when migration is expected.

Ideally, an effective tag should have the following characteristics:

(a) It should be retained through successive moults for up to three years. Some slight losses might be acceptable but these must be measured if the tag is to be used in quantitative studies.

(b) It should not increase mortality. Losses at the time of tagging should be distinguished from subsequent deaths (e.g. at moulting).

(c) It should not depress the growth rate (either by delaying moulting or by reducing the growth increment at the moult).

(d) It should not impair mobility or behaviour. Any such effect could lower survival (e.g. by increased predation), reduce the likelihood of recapture, or change the pattern of migration or dispersal.

(e) It should be recognized easily by fishermen. Not only is it necessary to have all tagged rock lobsters reported, but also it is important that they be identified at sea (so that locality and depth can be recorded) rather than at the processing plant.

Tags were tested initially in aquaria and if showing promise, field trials were carried out upon readily accessible reefs in a test area. In the earlier tests (1964-68), the closed-circuit seawater system situated some kilometres from the sea did not afford ideal conditions, but the main effects of the tags could be gauged by the use of untagged controls. From 1969, an open-circuit seawater system was available at the new laboratory on the coast.

TAG TESTS

1. Tag cut from rigid plastic sheet

This type of tag (see Figure 1) has been used to some extent in South Africa upon *Jasus lalandii* (Milne-Edwards) by Heydor~~d~~n (personal communication) and also in Cuba upon *Panulirus argus* (Latr.). Samples obtained from South Africa were tested on aquarium held western rock lobsters. Eighteen juveniles were tagged by inserting the barbs into the dorso-lateral muscles between the second and third abdominal segment, and held with eighteen untagged controls.

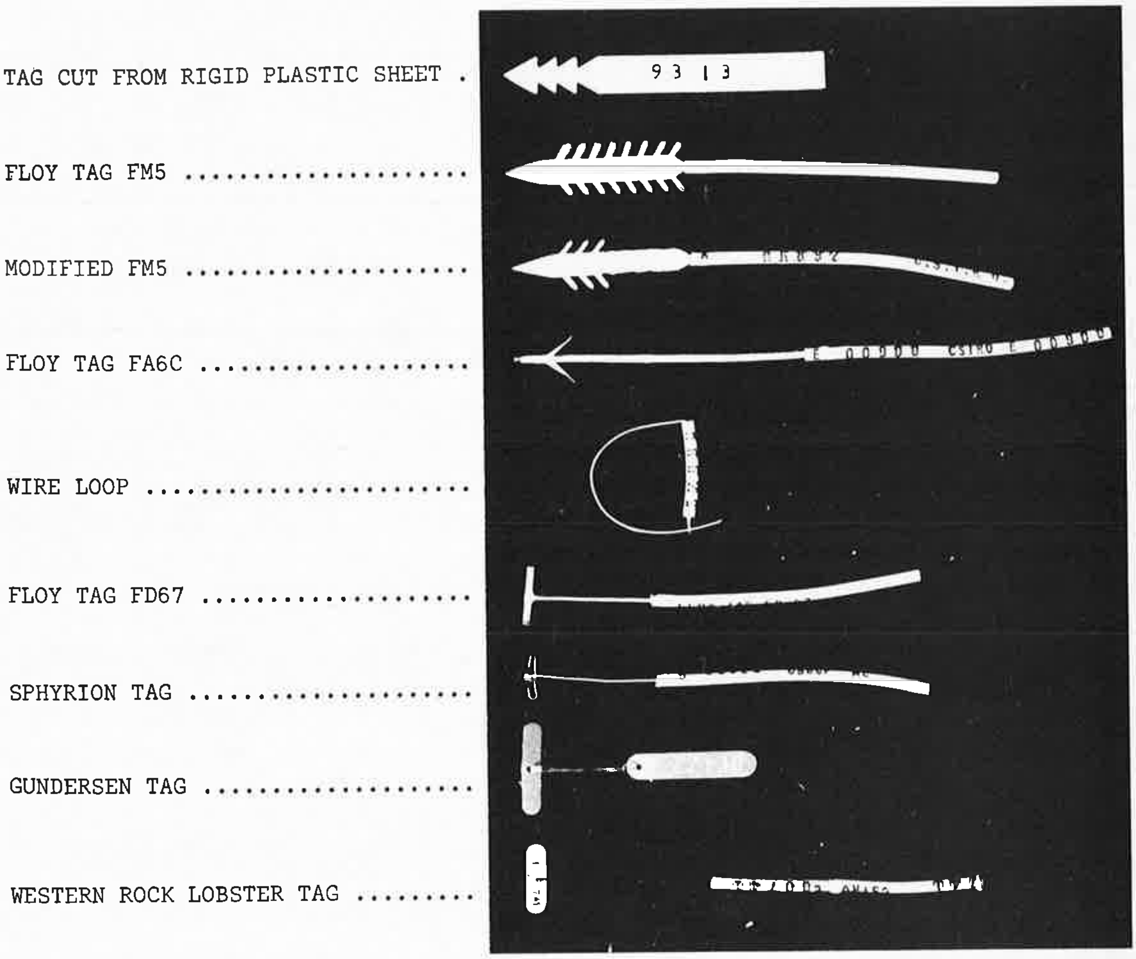

Fig. 1. Some of the tags tested for use on the western rock lobster (0.85 actual size).

There was much bleeding as the tags were inserted and the area around the tag often became severely infected, although only one specimen died as a result. The rigidity of this tag was a disadvantage, rock lobsters backing rapidly in a fright reaction often striking the protruding end of the tag on a rock or the tank wall. This tended to re-open the wound, and in two cases, broke the tag leaving the barbed head in the muscles. Only three of the tagged rock lobsters moulted during the three months of this test. Tags were held in each case but the growth increments (1.0, 1.4, 1.7 mm) were much less than those of controls (3.0 - 4.7 mm).

Rock lobsters carrying this tag did not extend the tail as often or as fully as the controls. There appeared to be some loss of mobility which would be undesirable in the field as migration might be restricted and both survival and recapture of tagged individuals diminished.

2. Floy Tag FM5

This was one of a series of tags made by Floy Tag and Manufacturing Inc., 4616 Union Bay Place NE, Seattle, Washington 98105, U.S.A. This tag (Figure 1) has been used in Hawaii on *P. japonicus* von Siebold by Morris (personal communication) apparently with some success (recoveries up to 17 per cent).

Eighteen juvenile western rock lobsters were tagged with this tag and held with the 18 untagged controls. There was extensive bleeding as the tags were inserted. Six tagged animals died from four to nine days after tagging, the muscle around the tag being dark and necrotic. During the next few weeks, the numbered plastic tubing broke away from the head of three of the tags, making these ineffective.

When the test was terminated after 137 days, the remaining nine tagged rock lobsters had moulted once, seven shedding the tag (and one animal dying after moulting), so that only two of the original 18 tagged rock lobsters succeeded in carrying the tag through a moult. During the same period the controls all moulted successfully.

Once again, the tagged rock lobsters appeared to have difficulty in straightening the tail, a slight hump being evident at the point of insertion of the tag, even at the end of the test period.

3. Modified FM5

In an attempt to make the multibarb tag more effective, the last five pairs of barbs were removed, in the expectation that the wound would heal better behind the front three barbs. Thirty rock lobsters were tagged, half being first treated with antiseptic on the surface of the site of tagging.

Neither the removal of barbs nor the treatment with antiseptic made any improvement. Seven animals died three to four days after tagging, nine tags lost the numbered plastic tubing, seven tags were shed during the first moult, three held the tag through the moult but died within 48 hours, leaving four from the original 30 surviving with the tag intact after one moult. The growth increment at moulting of the tagged specimens was less than that of the untagged controls.

4. Floy Tag FA6C

This single barb tag has a long shaft specified by Olsen (personal communication) for use on the southern rock lobster *Janus novaehollandiae* Holthius. In a test of this tag, 18 juvenile rock lobsters were tagged and held with untagged controls of the same size range. Two tagged animals died after tagging (at four and eight days), the muscle around the tag being severely infected. By the 105th day after tagging, the remaining 16 tagged rock lobsters had all moulted but 13 had either shed the whole tag or lost the numbered plastic tubing. Three retained the tag through the moult, but two died within a few days, apparently as a result of infection through the re-opened tagging wound. Thus only one of the 18 survived a moult with tag intact. The untagged controls moulted without any deaths.

During 1964, B.K. Bowen (personal communication) carried out a field trial of this tag (FA6C) at the Abrolhos Islands. A total of 1199 western rock lobsters were tagged and also marked with an arrow-shaped tail punch, while 912 received a heart-shaped punch mark on the telson but were not tagged. Comparison of recovery rates from the two groups (within the same ree~~d~~f area) indicated that in two months at least 64 per cent of the tagged rock lobsters had either died or lost their tags. Mutilation of tags was higher in the field than in aquarium tests. In one series of 90 tags recaptured approximately two months after tagging, the plastic tubing of 32 was so bitten that the tag number could not be identified.

5. Wire loop

This was modified from the Suture Tag of Edwards (1965). In a preliminary trial (carried out in the closed-circuit system during 1965), a loop of suture wire 0.2 mm diameter was inserted through the dorsal muscles between the carapace and the first abdominal segment using a curved needle. A short length of plastic tubing over the exposed portion of the loop carried the number identification. The splitting of the membrane immediately behind the carapace at ecdysis was expected to favour retention of this type of tag.

Ten juvenile rock lobsters tagged in September all survived the initial tagging and moulted during the following eight weeks. Only two tags were shed at the moult. Growth increments may have been depressed but loss of controls prevented a proper comparison. The preliminary trial was sufficiently encouraging to warrant further tests.

Early in 1966, a further test of the wire loop tag was commenced, the stainless steel wire being 0.6 mm in diameter, rigid enough to be inserted without using a needle yet soft enough for the free end to close the loop easily (Figure 1). Fifteen juvenile rock lobsters were tagged immediately behind the carapace as before and held in the closed-circuit aquarium. Little bleeding occurred during tagging and little infection occurred subsequently.

One rock lobster died four days after tagging and the tag was torn from another specimen within one month of tagging (not having moulted). The remaining 13 held the loop tag through the first moult but three animals died soon after moulting. At least one of these deaths was due to a temporary failure in water circulation (moulting rock lobsters being highly sensitive to a decreased oxygen supply). The remaining ten tagged specimens all survived a second moult, only one shedding the tag. Growth increments (mean 2.80±0.34 mm at first moult, 2.35±0.76 mm at second moult) were not particularly good, but comparisons could not be made owing to circulation problems in different tanks. However, the relatively good retention of the loop tag led to a field trial on one of the test reefs.

In February 1967, a total of 146 juvenile rock lobsters were tagged with loop tags and returned to a small section of reef in the test area at Garden Island (32°10'S., 115°39.5'E.). Other juveniles were tail punched and pleopod clipped on adjacent segments of reef for growth and census measurements.

During September, 301 rock lobsters were trapped on the section of reef where the tagging had been carried out. Of these, 38 carried loop tags and four more carried scars or remnants of wire showing that they had been tagged. Many other rock lobsters (1329 animals) were trapped on adjacent segments of reef during September and October, none of these carried loop tags, showing that there had been practically no dispersal of tagged individuals away from original reef site during that period.

The total population of rock lobsters inhabiting the tagging site in September was estimated to be 382±78 animals. This was calculated by the single census method, marking (pleopod clipping) independently of the loop tags. Assuming that 38/301 of this reef population carried loop tags, the total numbers of tagged rock lobsters surviving to that date would be 48. The natural mortality coefficient of juvenile rock lobsters in this area, measured as described by Chittleborough (1970), on an adjacent segment of reef between January and September 1967, was .026 per week. Then in the 29 weeks between tagging and recapture, the group of tagged rock lobsters would have been expected to decrease from 146 to 69 by natural mortality. The number calculated to have survived was 48 tagged rock lobsters, so that the estimated tagging mortality was 21/69 or 30.4 per cent over the period of 29 weeks.

From the condition of tags and tagging scars at the time of recapture, loss of tags could be expected to continue, and also further deaths would occur as tearing during moulting had resulted in some tag sites becoming re-infected. The rigidity of the wire had caused distortion of the posterior margin of the carapace during moulting of some specimens, the buckling sometimes interfering with the precise measurement of carapace length.

Growth (increase in carapace length) of 24 rock lobsters which carried the loop tag intact for the 29 weeks ranged from 0 to 4 mm with a mean of 2.2 mm. This represented poorer growth than that of 108 rock lobsters recaptured at the same time, after tail punching at the beginning of the year. In these, growth ranged from 1 to 11 mm with a mean of 6.6 mm.

Despite some initial promise, the wire loop tag did not prove to be sufficiently good to warrant further development.

6. Floy Tag FD67

This type of tag has been used to tag teleost fish (Lenanton, personal communication) and also prawns (Lucas, Young and Brundritt, 1972; Penn, personal communication).

Twelve juvenile rock lobsters were tagged in February, 1968. The anchor bar of the tag was injected into the dorso-lateral muscles between the carapace and the first abdominal segment. No deaths occurred immediately after tagging, but four died when the circulation failed five weeks later. Dissection of the dead specimens showed that two of the tags would have been lost shortly. Of the surviving eight tagged rock lobsters, one lost the tag without moulting, six shed the tag during the first moult, while the last remaining animal held the tag through the moult but died next day when the water circulation failed.

This type of tag appeared quite unsuitable for the western rock lobster.

7. Gundersen Tag

This was first used by Gundersen (1962) on the crab *Cancer pagurus* (L.) and later on the lobster *Homarus vulgaris* (L.). Mohamed and George (1968) have also used this tag on *Panulirus homarus* (L.) with some success.

Twelve juvenile western rock lobsters were tagged by inserting the anchoring toggle into the muscle dorso-laterally between the carapace and first abdominal segment. This test was commenced during February 1968, in the closed-circuit seawater system using tags obtained from Norway. Two animals died without having moulted. The remaining ten all retained the tag successfully through the first moult. Seven moulted again before the test was terminated, each retaining the tag. The untagged controls were lost due to a circuit fialure early in the test, but the mean growth increment per moult of the tagged animals (3.04 mm) compared favourably with that of controls from tests in previous years in the same seawater system.

Early in 1969, another test of this type of tag was commenced (in the new open-circuit seawater system). On this occasion, the tags were made locally so that the test was partly to check the effectiveness of the sheet plastic from which the tags were made.

Twelve juvenile western rock lobsters (carapace lengths ranging from 42-52 mm in an attempt to use a single age group) were tagged as before, and held with twelve untagged controls of similar size. Because they were also part of another experiment on feeding rates, both groups were fed three times a week. This has some bearing on the interpretation of the results.

During the 44 weeks of this test, all the rock lobsters moulted, most moulting twice, some three times. The twelve tagged animals underwent a total of 25 moults without any deaths occurring. Only one tag was shed (at that individual's second moult). The twelve controls also achieved a total of 25 moults with no deaths occurring. Tagging did not depress the frequency of moulting. The growth increment per moult of the tagged rock lobsters (range 0.1 - 5.3 mm, mean 2.7 mm) did not differ significantly from that of the controls (0.0 - 4.9 mm; 2.7 mm). However, in both groups, the moult increments were less than in other rock lobsters which had been fed daily.

The aquarium tests were sufficiently encouraging to warrant a field trial of this type of tag. In January, 1970, a total of 207 juveniles (carapace lengths ranging from 40-80 mm) were tagged and released in one segment of reef in the test area at Garden Island. Each was given a secondary mark by clipping one of the abdominal spines. On an adjacent reef, marking (by clipping another spine) was carried out in order to compare mortality on the two reefs and tail punching was also carried out to compare growth rates.

Recaptures after four weeks showed the tags to be holding well and in good condition but this was to be expected as most animals had not yet moulted since tagging. One defect was that on some tags, the printing was lifting from the plastic. This was more serious after twelve weeks (Table 1), but by that time, a much greater problem was becoming evident. The external portions of many of the tags apparently had been chewed by other rock lobsters, obliterating the printing and even cutting off the plastic plate completely. This problem increased with time so that after 42 weeks, less than 8 per cent of the recaptured tagged animals could be identified. However, Table 1 shows that the field trial confirms the low losses by shedding of the whole tag (mainly at moulting), already indicated in the aquarium tests.

This test underlines the need for field trials of tags, rather than to rely completely on aquarium tests. In the aquarium tests, tagged rock lobsters were held in small groups furnished with individual shelters so that mutilation of the tags was not a serious problem. However, in wild populations, the gregarious behaviour of these rock lobsters led to much more mutilation of tags by biting and chewing. This appeared to increase further under stress conditions when a group was confined in a trap.

At the first moult after the trial commenced, the mean growth increment of the tagged rock lobsters did not differ significantly from that of the tail punched animals.

The natural mortality coefficient measured (as described by Chittleborough, 1970) during 1970 on a reef adjacent to that of tagging was 0.09×10^{-2} per week. Then at 34 weeks after tagging, natural losses would have reduced the tagged group from 207 to 200 individuals. The total stock on the tagging reef at 34 weeks (measured by single census method not using the tags) was estimated to be 410±48 rock lobsters. As 71/192 of these had been tagged (Table 1), the total number of the tagged group surviving after 34 weeks was 152 animals. Thus, of 55 deaths occurring in the tagged group over the 34 week period, 48 were caused by the tag. This represents a tagging mortality of 24.0 per cent.

The most serious defect in using the Gundersen Tag on western rock lobsters was the mutilation of the external segment of the tag. In an attempt to overcome this, the flat plate was replaced with plastic tubing carrying the identification number. Tests of these modified Gundersen Tags were carried out at the same time as the field trial of the Sphyrion Tag reported below.

8. Sphyrion Tag

This tag was developed by Scarratt and Elson (1965) for use on salmon and lobsters and later applied in research upon *Homarus americanus* (Cooper 1970, Scarratt 1970). It was used by Little (1972) on *Panulirus argus* though recaptures in this species were low and did not extend over a long period.

After the high loss rate of Floy Tag FD67 from western rock lobster, it was thought unlikely that the Sphyrion Tag would be satisfactory for this species as the anchoring toggle was no larger than that of Floy Tag FD67. A relatively small test was set up in constant temperature aquaria (at 26°C), eight juvenile rock lobsters being tagged dorso-laterally immediately behind the carapace using the Sphyrion Tag. Three animals died a few days later, but this was apparently due to oxygen deficiency because of poor circulation of water, rather than from infection at the site of tagging. The remaining five tagged animals achieved a total of ten moults without shedding a tag, a better result than had been anticipated.

Accordingly, a field trial was set up, in which the effectiveness of the Sphyrion Tag was compared with a modified Gundersen Tag (toggle of flat plastic, 14 x 3 x 0.6 mm, as before, but external flat section replaced with plastic tubing carrying identifying number). The anchoring ability of the Gundersen Tag had been verified, but the modification was aimed at lessening mutilation of the external portion by other rock lobsters.

During January, 1971, in the test area at Garden Island, 195 juvenile rock lobsters were tagged with the Sphyrion Tag and 183 others with the modified Gundersen Tag. During the same month, 314 juveniles were tagged on a test reef at Seven Mile Beach (29°08'S., 114°53'E.) using the modified Gundersen Tag. As a means of checking on tag loss,

TABLE 1

TRIAL OF GUNDERSEN TAG ON TEST REEF AT GARDEN ISLAND. RECAPTURES SUBSEQUENT TO TAGGING 207 JUVENILE WESTERN ROCK LOBSTERS IN JANUARY 1970.

Weeks since tagged	Total catch	Total tagged recap'd	Tags still intact	Tags shed	Tags illegible	
					Printing lifted	Chewed
4	139	65	60	0	4	1
12	131	54	28	0	10	16
34	192	71	7	3	2	59
38	202	73	8	0	2	63
42	160	53	4	0	0	49

TABLE 2

COMPARISON OF RECAPTURES FROM TWO TYPES OF TAGS TESTED ON REEF C AT GARDEN ISLAND DURING 1971

Tag type	Numbers Tagged Initially	Time lapse to recapture									
		5 weeks		13 weeks		31 weeks		35 weeks		39 weeks	
		No.	%	No.	%	No.	%	No.	%	No.	%
Sphyrion Tag	96	27	28.1	37	38.5	38	39.6	20	20.8	20	20.8
Modified Gundersen Tag	93	27	29.0	33	35.5	34	36.6	19	20.4	18	19.4

TABLE 3

LOSSES FROM TWO TAG TYPES AT SUCCESSIVE INTERVALS DURING FIELD TRIALS ON JUVENILE WESTERN ROCK LOBSTERS

Tag - recapture interval (weeks)	Test at Garden Island						At Seven Mile Beach		
	Sphyrion Tag			Mod. Gundersen Tag			Mod. Gundersen Tag		
	Total recap.	Tag lost		Total recap.	Tag lost		Total recap.	Tag lost	
		No.	%		No.	%		No.	%
5	67	1	1.5	57	0	0	76	0	0
13	99	12	12.1	57	6	10.5	61	1	1.6
31	80	12	15.0	67	5	7.5	117	2	1.7
35	38	8	21.0	41	4	9.8	42	0	0
39	33	6	18.2	31	3	9.7	59	0	0
52	56	15	26.8	62	8	12.9	71	4	5.6

TABLE 4

PROPORTIONS OF RECAPTURED TAGS WHOSE EXTERNAL PLASTIC TUBING HAD BEEN MUTILATED BEYOND RECOGNITION OF TAG NUMBER

Tag - Recapture interval (weeks)	Garden Island			Seven Mile Beach		
	Total tags recap.	Chewed beyond identification		Total tags recap.	Chewed beyond identification	
		No.	%		No.	%
5	123	0	0	76	1	1.3
13	138	2	1.4	60	0	0
31	130	11	8.5	115	7	6.1
35	67	9	13.4	42	2	4.8
39	55	5	9.1	59	6	10.2
52	95	13	13.7	67	12	17.9

each individual tagged was given a secondary mark by clipping a spine, distinguishing the type of tag used and reef upon which released.

Mortality due to tag: In this case, it is only possible to compare the recaptures of the two types of tags and assume that the mortality generated by the modified Gundersen Tag was the same as that recorded in the previous section for the Gundersen Tag. Table 2 shows that very similar proportions of the rock lobsters originally tagged with the two different types of tags were recaptured each time re-trapping was carried out. Intense fishing over the whole test area twelve months after tagging resulted in the recapture of 28.7 per cent of those originally tagged with Sphyrion Tags and 33.9 per cent of those originally tagged with modified Gundersen Tags. This shows that the mortality generated on this species by the Sphyrion Tag was practically the same as that generated by the Gundersen Tag. (For this comparison, the retention or condition of the tag at the time of recapture was not considered.)

Tag loss: From the marked animals recaptured throughout the year following tagging, the proportion which had shed the entire tag was recorded (Table 3). After five weeks of freedom, very few tags had been lost because few of the rock lobsters had moulted in that time. After 13 weeks, when all of the juvenile rock lobsters had moulted once, 12.1 per cent of the Sphyrion Tags had been shed. This is the same loss per moult as recorded by Cooper (1970) from *Homarus americanus* tagged with the Sphyrion Tag. Losses of Sphyrion Tags continued at subsequent moults though at a slightly lower rate (7-8 per cent per moult) so that at the end of a year (during which these juveniles would have had an average of close to three moults each), 27 per cent of the Sphyrion Tags had been lost.

Losses of the modified Gundersen Tag also occurred during the first moult after tagging, but few were shed throughout the rest of the year (Table 3). This type of tag then has a distinct advantage over the Sphyrion Tag for use on the western rock lobster.

Table 3 shows that there was a clear difference in the loss rate of modified Gundersen Tags between the two reef areas in which it was tested. The same research staff applied the same tagging technique to juveniles of similar size in the two areas. There are differences between the two localities, both in habitat and in population density. If either of these cause the loss rate of tags to vary significantly, it will not be possible to apply a single measurement of loss rate to all localities.

Tag mutilation: As the numbered plastic tubing of the external portion of the Sphyrion and modified Gundersen Tags were the same, recoveries of the two types were pooled when considering mutilation (biting or chewing) by other rock lobsters. Marked animals which had shed the whole tag were not included for consideration here.

Table 4 shows that loss of identity of tags increased throughout the year, the problem being of similar magnitude at both localities.

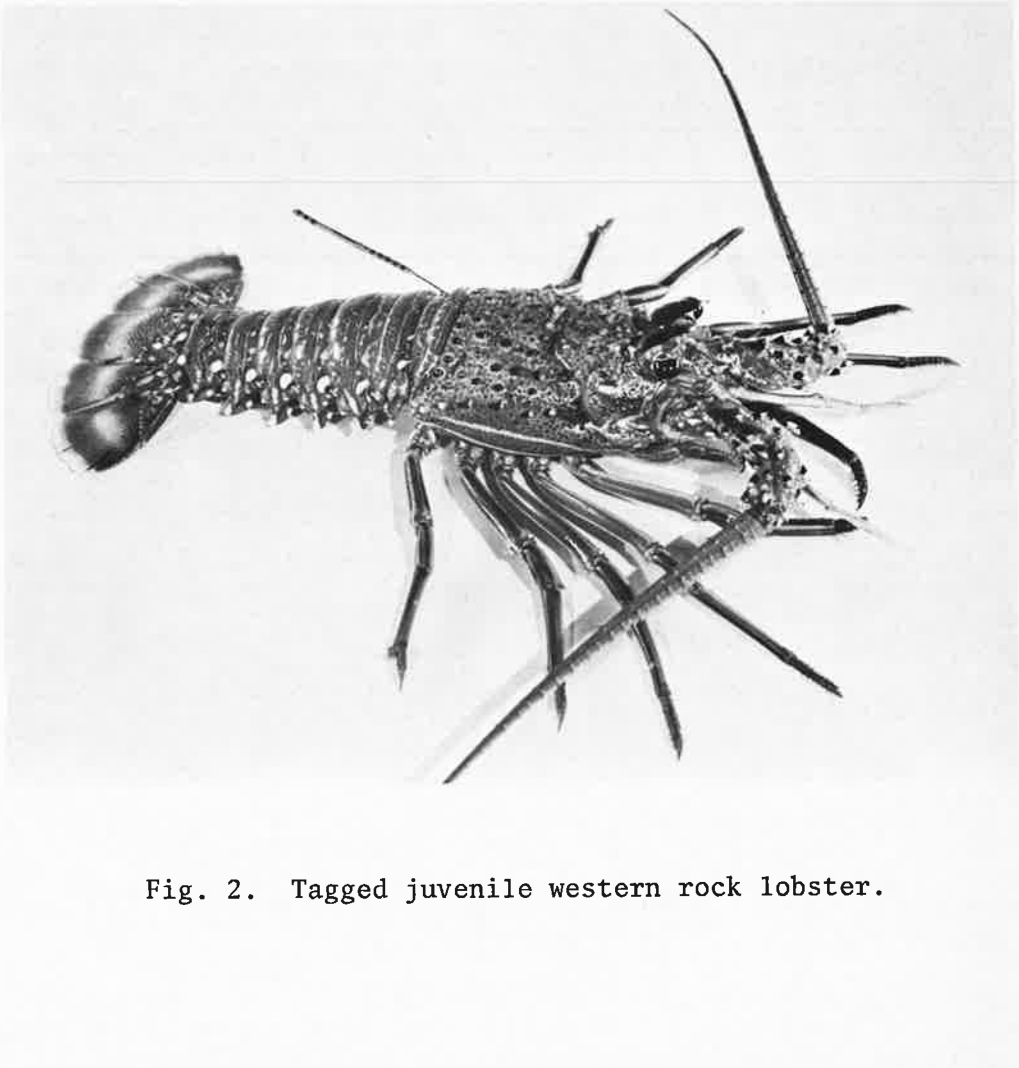

Fig. 2. Tagged juvenile western rock lobster.

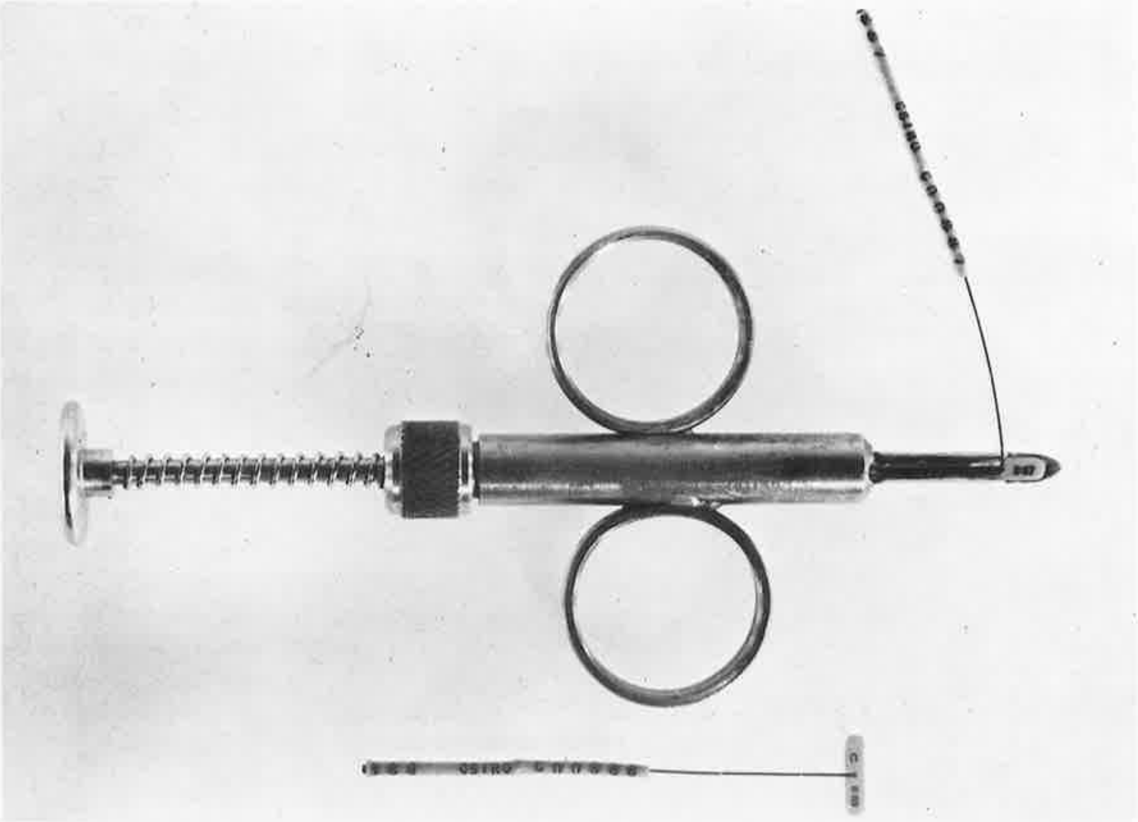

Fig. 3. Western rock lobster tags and applicator.

However, comparison of Tables 1 and 4 shows that the plastic tubing suffered far less mutilation than the flat plastic of the original type of Gundersen Tag.

Tagging and Growth: If tagging depressed growth, the effect is likely to be more pronounced at the first moult than at subsequent moults. Table 5 shows that the growth increment at first moult after inserting the Sphyrion Tag was slightly less than that after applying the modified Gundersen Tag, but this difference was not significant ($P>0.05$). Tail punching was not carried out at Garden Island during 1971, but the growth increments at first moult after tagging were only slightly less than those tail punched in previous years. However, direct comparisons are difficult owing to variation in moult increments from one year to another. These variations will be considered in detail in a separate study.

9. Western Rock Lobster Tag

The tag now in use for research on the western rock lobster (Figure 2) was developed from the tests described above. Because it was thought that the relatively long anchoring toggle (14x3x0.6 mm) might contribute to the mortality due to tagging (see Section 7 above), the toggle length was reduced from 14 mm to 11 mm. In order to overcome (at least partially) the problem of loss of tag identity due to mutilation of the external plastic tubing, the number was printed on the internal toggle as well as on the plastic tubing.

The flat toggle piece was made and numbered by Howitt Plastics Co. (Molalla, Oregon, U.S.A.), the numbered plastic tubing obtained from Floy Tag & Manufacturing (Seattle, Washington, U.S.A.), and the tags assembled at this laboratory. Polypropylene filament (dia. 0.3 mm) was selected to join the two sections as polypropylene melts back from a heat source to give a locking mass at the end of the filament without loss of strength. In assembling a tag, a double knot was first tied in the polypropylene filament and this knot pulled down inside the plastic tubing to the mid-point. This knot helped to lock the filament into the plastic tubing. The free end of the thread away from the numbered end of the plastic tubing was then cut leaving 2 mm of filament extending beyond the tubing. This free end was then held close to a heat source unitl the polypropylene melted back to form a lump just inside the tubing. The end of the plastic tubing also became swollen from the heat. This could be an advantage, making it more difficult for other rock lobsters to pass the free end of a tag between their mandibles. The filament was then cut 30 mm from the plastic tubing, and inserted through the central hole of the toggle section. By applying heat to the free end of the filament, a locking lump melted back, leaving the filament between the two numbered sections at approximately 27 mm.

These tags were inserted using an applicator (Figure 3) having a hollow, sharpened blade. The toggle was injected into the muscle to one side of the mid-dorsal line, between the carapace and the first abdominal segment. The plunger then ejected the toggle from the applicator. In practice, it was not found necessary to insert the toggle very deeply into the muscles.

TABLE 5

INCREASE IN CARAPACE LENGTH (mm) OF JUVENILE ROCK LOBSTERS AT FIRST MOULT AFTER TAGGING AT GARDEN ISLAND IN JANUARY, 1971

Tag type	Males				Females			
	No.	Range	Mean	s.d.	No.	Range	Mean	s.d.
Sphyrion Tag	31	2.6-6.5	4.25	0.95	50	0.5-5.5	3.62	1.08
Mod. Gundersen Tag	22	2.0-6.6	4.43	1.19	26	2.0-5.9	3.87	1.11

TABLE 6

INCREASE IN CARAPACE LENGTH (mm) OF JUVENILE ROCK LOBSTERS AFTER TAGGING AND TAIL PUNCHING AT GARDEN ISLAND IN JANUARY 1972

A. Growth increment at next moult

	Males				Females			
	No.	Range	Mean	s.d.	No.	Range	Mean	s.d.
Tail punch	21	2-7	5.52	1.33	19	1-7	4.42	1.57
W. rock lobster tag	11	2.6-7.7	5.29	1.44	15	0.8-6.1	4.14	1.45

B. Growth over 12 months

	No.	Range	Mean	s.d.	No.	Range	Mean	s.d.
Tail punch	14	5-17	10.07	3.29	9	6-15	10.22	3.67
W. rock lobster tag	11	4.3-18.7	10.28	5.19	17	5.5-14.5	9.73	2.83

During January, 1972, tags of this type were inserted into 157 juvenile rock lobsters on a test reef at Garden Island. Another 135 juveniles on the same reef were marked by tail punching. Because of a residue of previous marking and tagging trials in the test area, it proved difficult in this instance to separate mortality due to the tag, shedding of tags (at moult), and those whose numbered plastic tubing had been chewed beyond recognition. However, an estimate could be made of the survival of tagged rock lobsters through all three forms of losses by comparing the ratio of those tagged and tail punched in January (157:135), with the corresponding ratio in the catch taken in October, 39 weeks later (36 intact tags:40 punched). Had there been no deaths due to tagging, loss of tags at moulting, or chewing of numbered plastic tubing, 47 tagged animals should have been recaptured in October to maintain the original ratio. This represents an overall tag loss of 23 per cent over the period of 39 weeks. Corresponding tag loss of the modified Gundersen Tag over a period of 34 weeks was estimated to have been 41 per cent (24 per cent dying as a result of tagging, approximately 10 per cent of the survivors shedding the tag and some 11 per cent of the remaining tags mutilated). On this basis, the western rock lobster tag represents an improvement on the modified Gundersen Tag.

This field trial enabled the effect of the western rock lobster tag on growth rate to be checked. At the first moult, the mean increments of the tagged males and females were both slightly below those of the tail punched controls (Table 6), but the differences were not significant ($P>0.05$). After one year of freedom on the test reef, the total growth of those tagged and tail punched (Table 6) again did not differ significantly. Thus the western rock lobster tag can be used reliably for studies of growth in this species.

It is of interest to note that the mean growth increments per moult recorded in Table 6 are higher than those of Table 5. In some cases, for example, the Sphyrion Tag test of 1971 vs. those tail punched in 1972, the differences were significant (for males, $P<0.001$; for females $0.01<P<0.05$). However, it is not clear whether such differences can be attributed to improvements in marking technique or to real differences in growth of rock lobsters at Garden Island from 1971 to 1972. This underlines the need for uniform controls in all such trials.

DISCUSSION

Most of the tags tested on the western rock lobster failed to meet one or more of the requirements listed in Section I.

In the development of an efficient tag for use in research upon this species, it soon became clear that the abdominal tergites of this species fitted too closely together to permit tagging between them. The dorso-lateral muscles immediately behind the carapace afford a suitable tagging site, but in this species, a relatively large anchoring toggle is required.

The shaft of the tag needs to be thin and flexible, otherwise the rear edge of the carapace becomes buckled at ecdysis.

The western rock lobster is highly gregarious, and individuals apparently clean off raised epiphytes growing on the exoskeletons of their fellows, leading to a problem of mutilation of tags by chewing. Tags having flat external sections are more vulnerable than those having plastic tubing; flexible shafts to the tags may also keep the external section down against the body, and thus less likely to be chewed by other rock lobsters.

Colour preferences were not tested in the tagging trials. Most of the tags tested were orange in colour. It may have been coincidence that the worst chewed tags were white (locally made Gundersen Tags).

The tag described here as the Western Rock Lobster Tag is the most effective available at present for this species. It has a high reliability for studies upon growth and movements of rock lobsters. For quantitative studies (mark-recapture estimations of population density), some further calibration of tagging mortality and loss rate at moulting is desirable. This would entail tagging (with a secondary mark such as spine or pleopod clipping) on a reef and a set of untagged controls distinctively marked (by another clipping or tail punch). This should be set up at the beginning of a year and comparative survival rates followed through successive re-trapping (releasing again after examination).

Because of possible differences in loss rates from one locality to another (Table 3), quantitative tests could well be carried out in several localities. When using the Western Rock Lobster Tag on breeding females at Abrolhos Islands, G. Morgan (personal communication) observed that tag losses were apparently higher than recorded in the tests on juveniles in shallow coastal reefs.

These tags are now being used in studies upon growth and movements of juvenile rock lobsters. Over 2300 juveniles have now been tagged. Owing to the size of the toggle used (11x3 mm) only those rock lobsters having a carapace length of 40 mm or more were tagged. By concentrating the tagging in test areas closed to commercial rock lobster fishing, some individuals have been re-trapped, examined and released up to 13 times since being tagged 31 months previously. Others have travelled up to several kilometres and recaptured by commercial fishermen.

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Western Rock Lobster Reared to Maturity

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Abstract

Young of *Panulirus longipes cygnus* have been reared in captivity from the puerulus phase to adulthood. Improved growth rate in captivity resulted in larger size at maturity and eliminated differences in growth between juvenile males and females evident in the feral population, but did not result in earlier maturity. Ages at first breeding ranged from 4·9 years to 5·7 years.

When held at 25°C, repetitive breeding occurred, in contrast to seasonal breeding in the wild population. Ecdysis did not always occur between each breeding cycle, but a fresh mating was required for the fertilization of each batch of eggs spawned.

Introduction

As far as is known from the literature, no species of the Palinuridae has been reared in captivity to maturity, so enabling the age at first maturity to be determined with precision. In the case of the western rock lobster, *Panulirus longipes cygnus* George, indirect evidence indicated that the age at maturity is in the vicinity of at least 5 years. This was mainly based on the progression of modal size from a strong year class through successive years within a shallow nursery area (Chittleborough 1970).

In October 1968, a group of puerulus larvae of the western rock lobster taken from artificial seaweed collectors (Phillips 1972) was brought into the aquaria at the Western Australian Marine Research Laboratories. As the wild population of the western rock lobster has a clearly defined breeding season (Chittleborough and Thomas 1969), the time of hatching of these specimens can be taken as the midpoint of the breeding season prior to their settlement on the artificial seaweed collectors. On this basis, the birth date of these specimens was taken as 1 January 1968, and the newly settled larvae were 0·8 years of age when collected. The mean carapace length of puerulus larvae is 8·3 mm (Phillips 1972).

Most of these larvae moulted within a few days of their capture, from the transparent puerulus to the pigmented post-larval phase. Individual records were not kept during the first post-larval year, some 30 specimens from the same source being held in the one tank and fed liberally on mussels, abalone, or fish pieces. At that time, the water in the open circuit seawater system was not heated, temperatures varying with the adjacent inshore seawater, ranging from 24°C in summer to 16°C in winter.

Later, these were used as part of a stock of juveniles for various experiments designed to measure the effects of different environmental conditions upon growth and survival. The results of these experiments are being described separately.

During the second post-larval year, specimens were held at various constant temperatures (20, 23, 26, 29°C). Detailed records including the date of each moult and the carapace length after moulting, were kept for each rock lobster from the commencement of that experiment. In subsequent years they were maintained at 25°C, the optimum temperature for this population (Chittleborough, unpublished data).

Six of the original group of larvae were retained to maturity, being held together in one large tank (still at 25°C) since March 1972. As the case history of each is known in detail, they afford the first direct measurements of age at maturity.

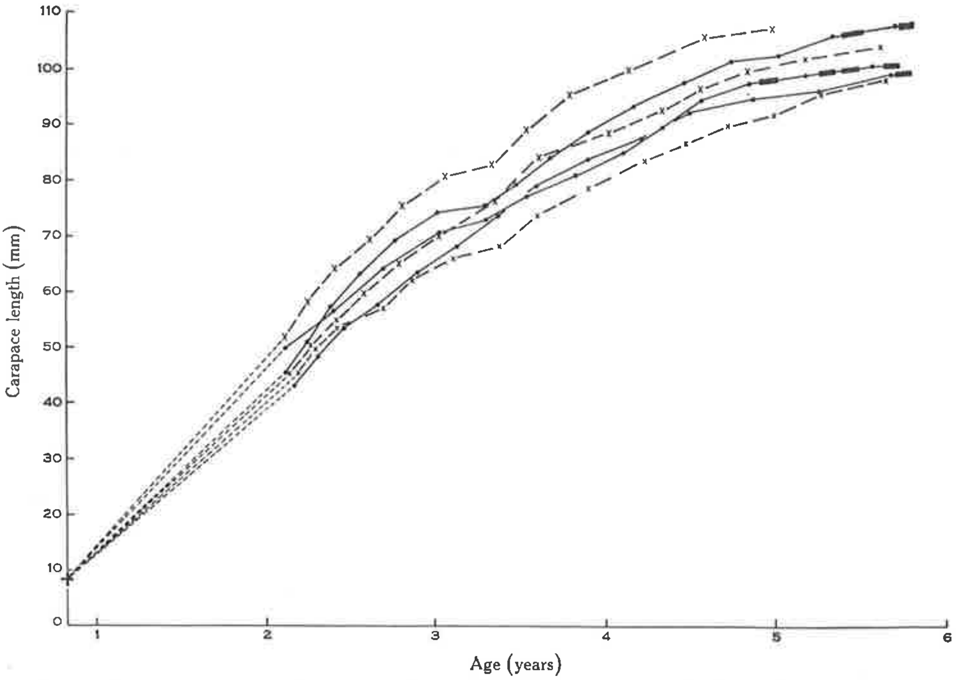

Fig. 1. Size at each moult of male (×) and female (●) western rock lobsters reared from puerulus larvae (+) to breeding (flat solid rectangles). Individual moults not recorded in first post-larval year.

Growth

At this stage, only a general outline of the growth of these animals will be given for comparative purposes. The growth of the six specimens is summarized in Fig. 1. Both the frequency of moulting and the growth increment per moult decreased from the age of 2+ years to 5+ years (Table 1).

The growth of these aquarium held specimens differed from that of reef dwelling rock lobsters in several respects. Not only was the growth more rapid than in the wild population, but also under the more favourable conditions (abundant food supply; higher temperature), there has not yet been any significant difference in growth rate between the sexes. In the wild population, growth rate of males has been shown to be significantly greater than that of females from as early as 3 years of age (Chittleborough, unpublished data).

As the data shown in Fig. 1 were from specimens held at constant temperature, there was no seasonal variation in growth rates. Four of the lobsters experienced a temporary diminution of growth rate at just over 3 years of age. This followed immediately after their transfer from one tank to another, and perhaps more important, placing together specimens which had not been associated during the previous 12 months.

Table 1. Moulting frequency and growth per moult (carapace increment) by age groups for western rock lobsters reared in captivity

Age (yr)	Number of moults		Growth (mm) per moult	
	Range	Mean	Range	Mean
2+	3–6	4·8	3·6–7·6	5·29±0·33
3+	3–4	3·8	1·1–7·3	4·66±0·68
4+	3–4	3·5	1·8–5·6	3·83±0·43
5+	2–3	2·6	1·1–3·8	2·31±0·56

Size and Age at Maturity

For the males, sexual maturation cannot be diagnosed properly unless specimens are killed. Behavioural changes in the males were not sharply defined, and in any case, probably reflected pheromone production from maturing females. It can be inferred that males mature at the same time or earlier than the females, since all individuals were the same age and the females were mated as soon as receptive.

Maturation of females might be taken as either (1) extension of the setae on the endopodites of the pleopods (necessary for carrying eggs), (2) mating (deposition of sperm mass on sternum of female), or (3) spawning. The inner segments of the pleopods became more setose at each moult during the fifth year of life, setae increasing from approximately 10 to 15 mm in length at the moult preceding mating of two of the females. However, while the setae of the third female reached 15 mm in length at about the same age, two further moults occurred before mating took place.

The time of first mating is the clearest indication of maturity, as spawning followed soon after. On this basis, one female matured at 4·9 years of age, the second at 5·4 years and the third at 5·7 years.

Because of the more rapid growth rate achieved by these specimens in captivity, the size at first maturity (97–106 mm) was considerably greater than the mean size of 76 mm recorded by George (1958) for the first breeding in the wild stock.

Breeding

As the females matured, the largest of the three males was the more aggressive and carried out the first mating. After his death (from injury during handling), the smaller of the two remaining males showed the greater sexual activity. This male was slightly smaller than the females with which it was mating (Fig. 1).

Since the sperm masses are deposited externally (on the sternum), there is no necessity for mating to be synchronized with moulting of the female in this crustacean. The shortest interval between moulting and subsequent mating was 14 days; other intervals range to more than 35 days.

Spawning occurred a few days after mating (under these aquarium conditions), but precise data are not available because females were only examined at weekly intervals in order to disturb as little as possible. In several cases, spawning occurred 2–3 weeks after mating.

As the breeding group was being disturbed as little as possible, incubation periods were not recorded exactly but appeared to occupy 20–30 days at this temperature (25°C). Incubation periods measured more precisely for three other adult females (of unknown age) held in aquaria at ambient sea temperature, were 58, 46 and 25 days respectively, the duration diminishing as the seawater temperature rose in spring from 18·5 to 23°C. These are similar to the findings of Berry (1971) for *Panulirus homarus*.

Eggs in each batch all hatched within the space of a few hours. Newly hatched larvae concentrated at the surface of the water. Because of the long larval period in this species (10–11 months) and the difficulties experienced by those attempting to rear larvae of other panulirids, no attempt was made to rear these larvae.

Under the conditions in which they were reared at this laboratory, the female western rock lobsters have bred repeatedly since reaching maturity. The first to mature has since completed seven breeding cycles in a period of 15 months, the second has completed five cycles in 11 months, while the third has completed three cycles in the 7 months since maturing.

A moult generally intervened between each breeding cycle, but on several occasions there were two cycles within one intermoult period. In most of these cases, a fresh mating occurred a few days after the hatching of the previous batch of eggs, but in two instances, the second spawning was not preceded by a mating. The old eroded sperm mass remaining from the earlier breeding cycle was inadequate for a second cycle as the eggs were infertile and were lost after about 3 weeks. Normal breeding cycles continued after a further moult.

At each moult following the hatching of larvae, the endopodites of the pleopods of these aquarium held females were as setose as during the previous breeding cycle. This is consistent with repetitive breeding and contrasts with the marked seasonal cycle in the wild population, whose females moult in the autumn to a non-breeding phase having non-setose pleopods.

The more active of the two males in this group of rock lobsters continued to show interest in females after they had spawned. However, ovigerous females always rejected such advances.

Discussion

Under favourable conditions in captivity (abundant food; optimum temperature), growth rate of juvenile western rock lobsters was enhanced, but this did not cause sexual maturity to be attained earlier than in the wild population. From this, it can be inferred that the relatively small mature females found on certain reefs are more likely to be stunted in growth than having matured at an early age.

It would appear that in the feral population, more intense competition for food causes an earlier divergence in growth rate between the sexes (from an age of 3 years) than in those afforded an abundant supply of food.

Repetitive breeding has already been demonstrated in natural populations of at least one of the tropical rock lobsters (Berry 1971). In that species (*Panulirus homarus*), repetitive breeding was more likely to occur in older (larger) individuals than in those recently matured. The ease with which young adults of *Panulirus longipes cygnus* reverted to repetitive breeding when held at relatively high temperature (25°C) may reflect relatively recent evolution from a tropical stock (George and Main 1967).

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Home Range, Homing and Dominance in Juvenile Western Rock Lobsters

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Abstract

Home ranges of juvenile western rock lobsters (*Panulirus longipes cygnus* George), measured on a relatively uncrowded reef over a period of one year, did not exceed a radius of 15 m. Tagged juveniles transferred to similar reefs seldom remained on the new sites. Some found their way back to the home reef (from distances of up to 400 m), while many dispersed at random, travelling up to 8·3 km in 9 weeks. Dominance for food is displayed amongst juveniles (aged 2–5 years), especially under crowded conditions.

The significance of these behaviour patterns is discussed in relation to research and management problems.

Introduction

As described by Chittleborough (1970), juveniles (aged 2–5 years) of the western rock lobster are concentrated mainly on shallow coastal reefs. Throughout most of the year there is little movement of juveniles from one reef to another. During the latter part of November and early in December (soon after the spring moult), the larger juveniles move out from the coastal reefs into deeper water, many of these being pale shelled juveniles locally called 'white' rock lobsters.

While there is minimal exchange of juveniles between reefs, little is known of the total area within which an individual forages, and whether each feeds randomly over the whole of a reef or establishes a definite home range. Also, it is not known whether those juveniles displaced away from their original reef, settle readily on another reef or make efforts to return to their original homesite, as has been described by Creaser and Travis (1950) for *P. argus* (transplanted individuals walking up to 9 km along the coast to return to the original reef).

The development of an efficient tag for the western rock lobster (Chittleborough 1974) has enabled experiments on home range and homing behaviour to be carried out in populations on natural reefs.

Chittleborough (1970) found when trapping juvenile rock lobsters for single census estimates of population density, that those aged 2+ years appeared to be less vulnerable to baited traps than older animals. At that time, it was not clear whether the younger individuals were dispersed in other habitats (e.g. the sea-grass beds), or were prevented from entering the traps because of some degree of dominance amongst juveniles. This has now been checked experimentally.

Home Range

During January 1971, when setting up a field trial at Garden Island of two different types of tag (Sphyrion Tag and modified Gundersen Tag; see Chittleborough

(1974)), it happened that on one of the test reefs, one type of tag was applied mainly to rock lobsters at one end of the reef and the other tag used mainly at the other end of that reef. At the time this was not thought to be particularly important. As the reef is relatively small (just over 100 m long and 25 m wide at the widest point), random foraging movements were expected to disperse the two types of tags over the reef. However, in subsequent re-trappings throughout the next 12 months, the pattern of distribution of the two types of tags remained much the same, indicating that a juvenile rock lobster may have a restricted home range while a resident of the shallow 'nursery' grounds. (Garden I., 32°10′S.)

Site	Number tagged
1	12
2	4
3	2
4	8
5	11
6	3
7	2
8	10
9	12
10	0
11	8
12	0
13	1
14	8
15	4
16	12
17	3
18	6
19	7
20	7
21	3

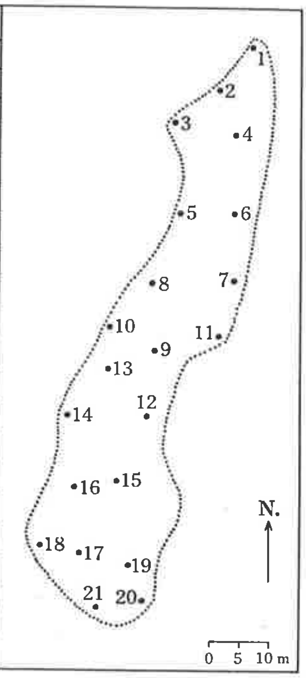

Fig. 1. Location of 21 trap sites on test reef at Garden Island, and numbers of juvenile rock lobsters taken at each site, tagged and released, in January 1972.

Following this observation, a more precise experiment was carried out during 1972 on the same segment of reef. Trap sites approximately 10 m apart were marked out using 21 cement blocks, each identified by a white plastic number on the upper surface. Because of the distribution of suitable sites for traps, and varying depth of water (0–15 m), the grid pattern established was not particularly regular (Fig. 1). During January 1972, 123 juveniles (mainly 3–5 years of age) taken from these sites were tagged with the western rock lobster tag (Chittleborough 1974), care being taken to release each animal as close as possible to the site of capture. The numbers tagged at each site varied considerably (Fig. 1), partly due to the presence of octopus in some of the traps.

During subsequent re-trappings after 1, 4, 8, 9 and 12 months from the time of tagging, the site of recapture was recorded in each case, and the tagged animals released (after re-measuring) on the site of recapture.

At the first re-trapping (4 weeks after tagging), other work limited traps to only seven of the 21 trap sites. Tagged individuals tended to move in from adjacent sites to the traps (Fig. 2). If it was assumed that the tagged animals had not strayed from the sites upon which they had been released 4 weeks earlier, then the radius of effect of a baited trap would be some 20 m. Because of this, traps should be placed simultaneously on all sites on the grid in order to demonstrate the usual home range of juvenile western rock lobsters.

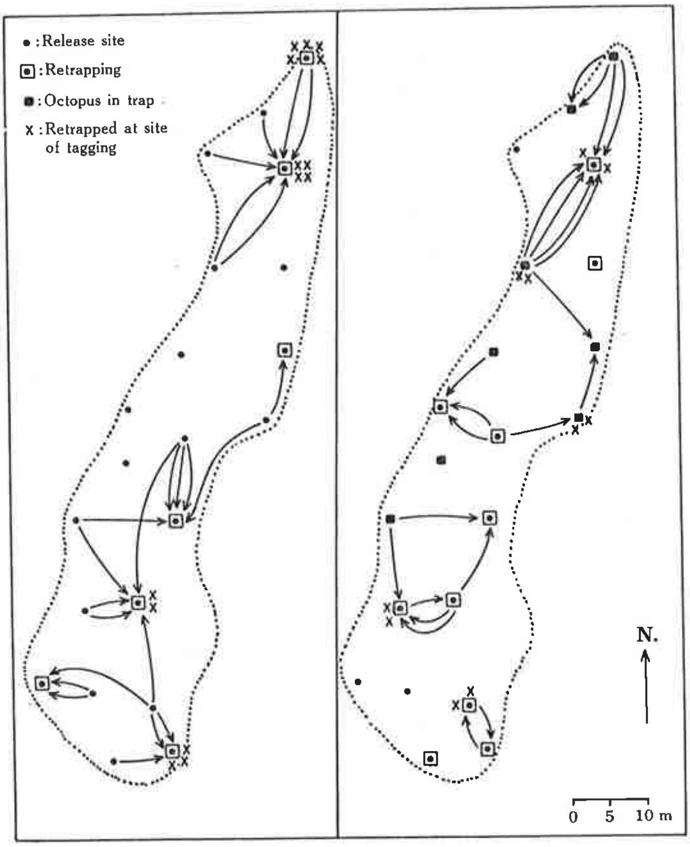

Fig. 2. Movements of juvenile rock lobsters on test reef at Garden Island after tagging in January 1972. Recaptures after 4 weeks (left) and 17 weeks (right).

At the second re-trapping (17 weeks after tagging), the presence of octopus in eight of the traps may have diverted rock lobsters to adjacent traps. However, of the 32 tagged rock lobsters recaptured (Fig. 2), the maximum movement from the tagging site was 16 m.

During subsequent recaptures over 12 months, there was little dispersion of rock lobsters over this reef. Table 1 shows that the degree of dispersion did not increase with time, a high proportion of the individuals remaining on the site of original capture. The greatest distance moved by any one animal was 30 m.

Some individuals were recaptured and released again several times throughout the year, enabling the area of their home ranges to be plotted. Fig. 3 shows the home ranges of 10 juveniles whose locations were recorded on 5 or more months during the year of this experiment. The maximum radius of the home range for any individual was 15 m.

Homing Behaviour

At the same time that the extent of home range was being measured, an experiment was carried out in the test area at Garden Island to determine whether the juveniles of this species display a homing instinct. Juveniles (aged 3–5 years) trapped on a reef adjacent to the gridded reef described in the previous section were tagged using the western rock lobster tag and released in batches on similar reefs at various distances along the coast away from the original homesite. Fifty tagged juveniles were transplanted 140 m south, 49 were released 400 m south, while groups of 50 were moved 400 m and 800 m north of the homesite. This was commenced early in 1972. Subsequent re-trapping was carried out throughout the test area to see whether the transplanted juveniles settled where released or moved in a particular direction. Fishermen operating slightly further offshore along the island were also alerted to watch for tagged rock lobsters.

Table 1. Juvenile rock lobsters tagged and released on marked sites of test reef in January 1972. Distances travelled when recaptured up to 1 year later

Dispersion (m)	Time (weeks) since originally tagged:					Dispersion (m)	Time (weeks) since originally tagged:				
	4	17	34	39	51		4	17	34	39	51
0	14	10	16	11	5	19	1				
7	6	5	3			20			1		
8	2	2	1	2	2	21				2	
9		2		3		22	1				
10	2	2	3	5	4	23					
11	3	1	3	1	1	24					
12		2	3	2	1	25					
13	1	1			1	26					
14	2	1		2		27				1	
15	2	2	1	2		28					
16	2	4	2	2		29					
17						30			1	1	
18	1				1	Total	37	32	34	34	15

Recaptures of transplanted tagged rock lobsters were much fewer than of those tagged and released on the reef of original capture. From the 199 juveniles transferred to other reefs, 20 have been recaptured. Only one had remained on the reef to which it had been transplanted (400 m south of the original reef), being recaptured 8 months later. Within 2 months of being transferred, four tagged individuals were recaptured back on their original homesite. Two of these had been released 400 m north, one 400 m south, and the other 140 m south of the original reef. Two more had moved towards their home reef; one released 800 m north was recaptured only 60 m north of the home reef (5 weeks later); the other released 140 m south was recaptured 4 weeks later 70 m north-west of the home reef.

The remaining 13 recaptures were all taken by fishermen operating off Garden Island, from 2–13 months after tagging. These juvenile rock lobsters had dispersed to the north, west and south respectively, following their transplanting to reefs relatively close to their home reef. Some individuals wandered rather quickly after being moved; one which had been moved 400 m to the north was recaptured 9 weeks later 8·3 km south-west of the home reef.

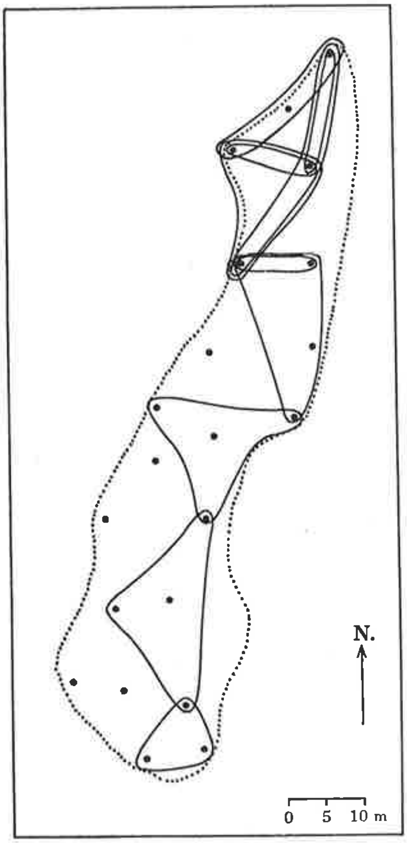

Fig. 3. Home ranges of 10 tagged juvenile rock lobsters trapped on test reef of five or more occasions throughout 1972.

These results indicate that juvenile western rock lobsters have a much poorer homing ability than *Panulirus argus* (Creaser and Travis 1950).

At the same time that these experiments were being carried out in the test area at Garden Island, another experimental transplant of juvenile rock lobsters was carried out further north along the coast. At Seven Mile Beach (29°08′S.), 299 juveniles (aged 3–5 years) were trapped, tagged, then moved 42 km south to Cliff Head (29°32′S.), where they were released on a group of 52 artificial shelters set in sea-grass beds several hundred metres away from natural reef. These shelters (hollow truncated pyramids made from asbestos cement) were readily occupied by rock lobsters when placed close to crowded reefs, so it was planned to establish a discrete population of known size, for other experimental work.

However, an underwater check of the whole group of artificial shelters carried out only 4 weeks after release showed that none of the tagged rock lobsters had remained in the shelters. During the 16 months following the release of these tagged rock lobsters, 26 have been recaptured by fishermen operating from Cliff Head.

These results show that when juvenile rock lobsters are moved away from their homesites, they do not readily settle, even on natural reefs comparable with the home reef, but disperse rapidly.

Dominance

An experiment giving some information on feeding dominance amongst juvenile western rock lobsters was carried out on the crowded test reefs at Seven Mile Beach in December 1972. Semi-circular screens were placed in front of both entrances of some of the baited traps. These screens consisted of wire mesh sold as 2 in. chicken wire. The width of the mesh varied from 43 to 61 mm. Aquarium tests showed that while 2-year-old rock lobsters could move through this mesh easily, many of the larger (older) juveniles could not.

Six traps carrying these screens and six unscreened traps were set out at random over the same segment of shallow reef, the test being conducted over one night only. Next morning, one of the screened traps contained an octopus, so was deleted from the test.

The size compositions of the catches taken by the screened and unscreened traps (converted to equal units of effort) are shown in Fig. 4. The catches taken by the unscreened traps were polymodal but the smallest size group (aged 2+ yr) was poorly represented. The catch rate of this age group was considerably higher in the screened traps, especially for the smaller individuals in the group (i.e. those under 34 mm in carapace length). The screens placed around the entrances of the screened traps selected against animals over 50 mm in carapace length.

Taking males under 42 mm and females under 40 mm in carapace length as the 2-year-old group (see Fig. 4), the mean catch per unit effort of 2-year-old rock lobsters in the screened traps (13·8 per trap-night) was significantly higher than that of the unscreened traps (6·5 per trap-night).

These results show that, although the smaller and younger individuals were abundant on the reefs in that area, competition for food resulted in a dominance of the larger juveniles preventing the smaller ones from entering the baited traps.

Discussion

The rapid dispersion of juvenile rock lobsters moved to other reefs shows that there was little inhibition of mobility as a result of tagging. Thus the very restricted movements of tagged animals replaced on their home sites cannot be attributed to loss of activity as a result of tagging.

The relatively small home range (maximum radius 15 m) measured on a reef in the test area at Garden Island during 1972 is not necessarily applicable to juvenile rock lobsters at other localities or in other years. At the time of the experiment, the density of the population in the test area was relatively low (1286±115 animals per ha in January 1972) in comparison with previous years (Chittleborough 1970). With less competition for food, individuals may not have found it necessary to forage over a very large area. On the more crowded reefs in the test area at Seven Mile Beach (population density 9374±1442 in January 1972), home ranges appeared to be larger, some marked individuals crossing the 50 m of sand and sea-grasses separating adjacent reefs.

Since none of the reefs in the test area at Garden Island were crowded during 1972, the failure of transplants to settle on the reefs to which they had been transferred cannot be attributed to competition for food or shelter.

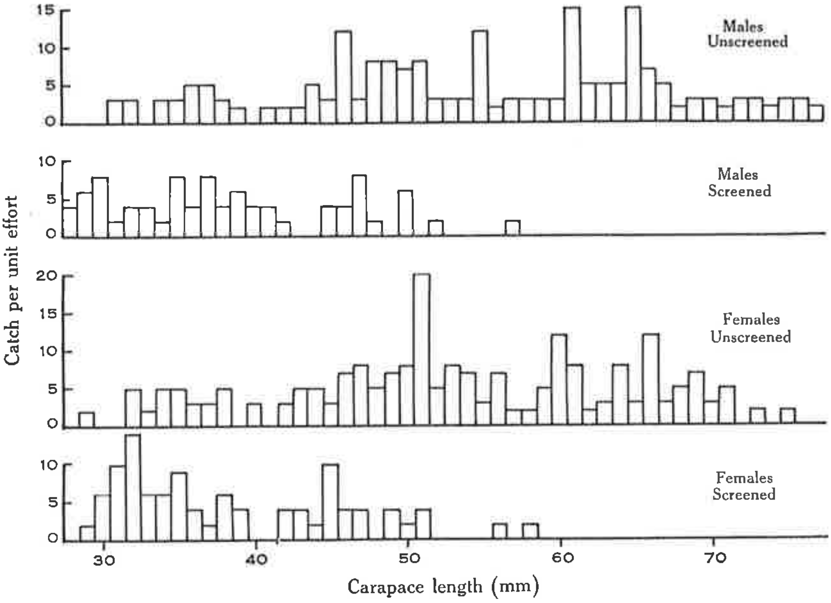

Fig. 4. Catch per unit effort for male and female rock lobsters taken in Seven Mile Beach test area by baited traps with and without screens (50 mm mesh) over entrances.

The rapid dispersion of these transplants has important implications both for research and for management of the fishery. When tagging for studies of migration, it is important that rock lobsters be returned to their original reef. Displacement beyond the normal home range is highly likely to result in abnormal movements of rock lobsters. This may have been overlooked in studies of migrations of other species.

Another aspect is that the wanderings of displaced rock lobsters could be expected to result in increased mortality, owing to greater exposure to predators. The lower returns of tags from transplanted groups when compared with returns from those released on the home reef might be due only to lower probability of capture after dispersion, but the high fishing pressures in surrounding waters indicate that the lower recapture rates are partly due to higher mortality. This underlines the value of the regulation requiring escape gaps to be fitted to all rock lobster pots and the need to encourage fishermen to return any undersized rock lobsters remaining in the pots to the reef of capture rather than to other reefs further along their lines of pots.

Because of feeding dominance amongst juvenile rock lobsters, estimates of population density by mark–recapture techniques relying upon baited traps tend to understimate the numbers of smaller animals (2 years of age). The effect of this probably varies with the relative proportions of the various age groups present at the time. Dominance would also intensify when the level of food supply was depressed. Shortage of food may be relative (depending on the density of rock lobsters) or absolute (reflecting fluctuations in the populations of food species). These aspects warrant further study.

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Review of prospects for rearing rock lobsters

by R. G. Chittleborough*

Studies at the Western Australian Marine Research Laboratories at Waterman near Perth show that there is no technical barrier to mass rearing of juvenile rock lobsters. Under optimal environmental conditions two-year-old western rock lobsters were reared to market size in an aquarium in less than half the time it would have taken in the wild state. However, before commercial pond farming of rock lobster is possible certain economic and legal barriers need to be overcome.

WHEN the possibilities of culturing rock lobsters were last considered (Chittleborough 1968), mass culture of larvae was thought to be impracticable.

Rearing of juveniles was technically possible, but the slow growth rate under natural conditions and the large quantity of food required then made this unattractive economically.

Because of the long and complex larval life, no attempts have been made since then to rear larvae of the western rock lobster (*Panulirus longipes cygnus*). As yet, no panulirid has been reared from egg to post larvae anywhere in the world, so that prospects for this form of culture remain extremely remote. However since the report of 1968, studies carried out at the Western Australian Marine Research Laboratories have resulted in greatly accelerated growth rate of juvenile western rock lobsters. The main purpose of these experiments, carried out in aquaria under controlled environmental conditions, was to gain a better understanding of the ecology of reef-dwelling natural populations, but the results also enable a fresh appraisal to be made of the prospects for pond raising juveniles of this species.

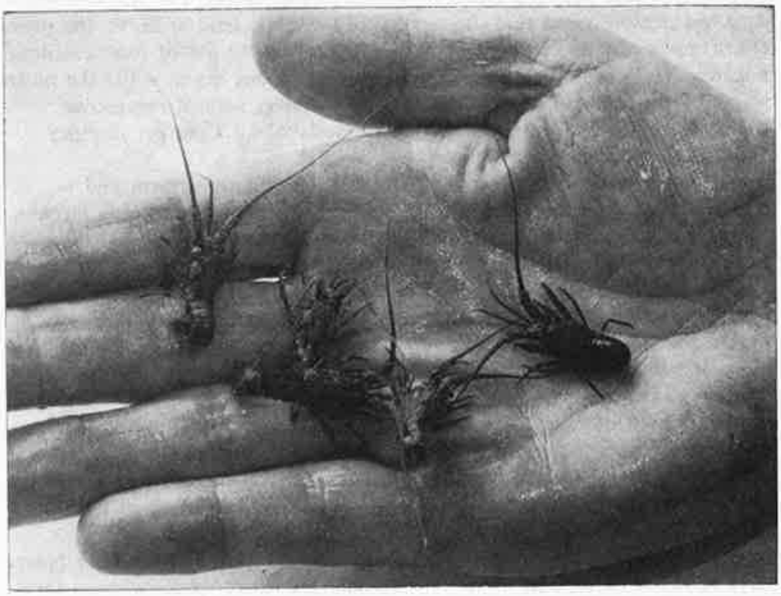
Optimum conditions for growth and survival

Temperature: Incoming sea water to the laboratory ranged from a maximum of 25.9°C in summer to 14.9°C in winter, resulting in a marked seasonal variation in growth rate of rock lobsters. When groups of juveniles were held at different levels of constant temperature throughout the year, growth rate increased with temperature up to 26°C, declining at higher temperatures. The main impact of temperature was upon the frequency of moulting rather than on growth per moult. Survival declined from 26°C, deaths usually occurring at the approach of or during a moult.

It was considered that a water temperature of 25°C was the optimum for growth and survival in this species.

Food: Although accepting a wide range of animals as food, the western rock lobster is a selective feeder, preferring shellfish to scale fish and the latter in preference to mammalian tissue. When offered pieces of both abalone and whiting, rock lobsters consumed over four times more abalone (weight) than whiting. Fresh food was preferred to stale.

When seeking an economical source of food for rock lobsters, a local pest species, the banded blowfish, was used in a feeding trial. When first offered pieces of blowfish, rock lobsters accepted eagerly, as had been observed when other species were offered as a variation to the diet. However, the rock lobsters soon lost interest in blowfish and in fact refused to eat it. Growth rate slowed down, and some individuals died of



Juvenile western rock lobsters being reared in the aquarium at the Waterman Laboratories. (Photo by Mike Brown, Australian Information Service, Perth).

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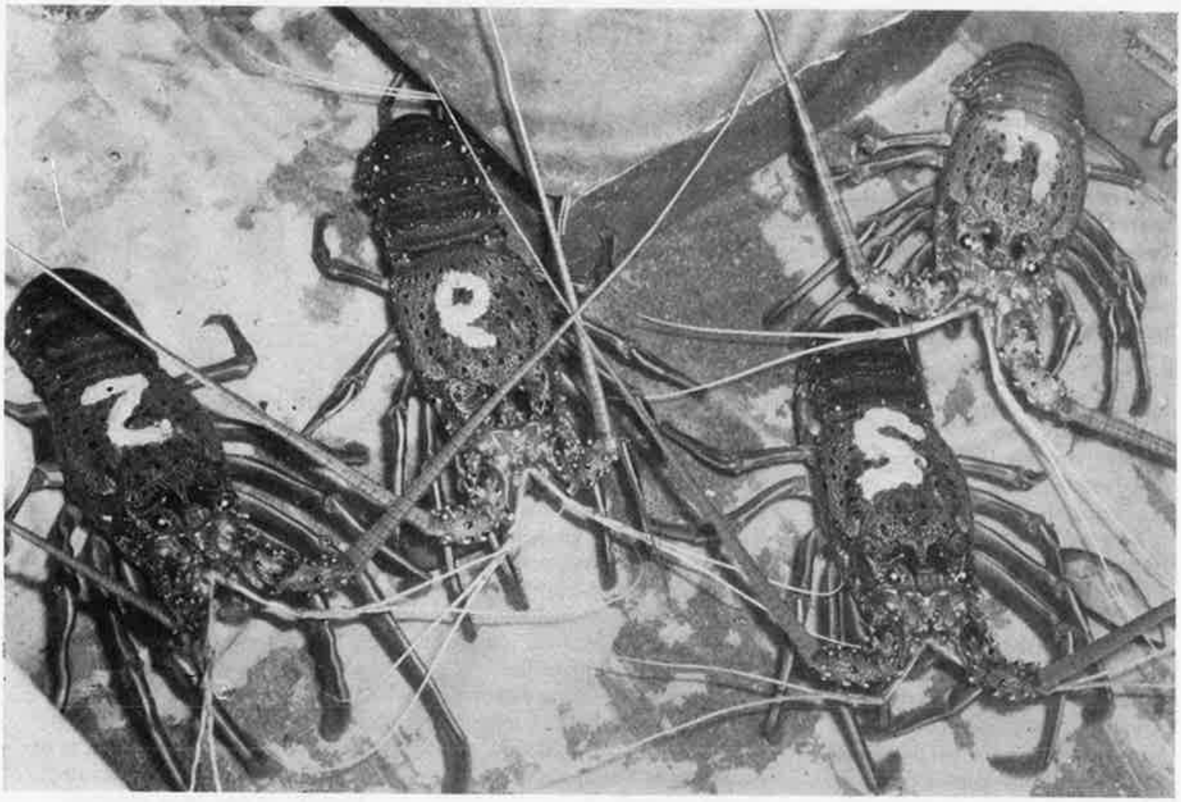


Adult western rock lobsters (six years of age) reared from puerulus larvae in a tank at the Western Australian Marine Research Laboratories. These specimens are now breeding actively.

starvation even though fresh pieces of blowfish were supplied daily. This test demonstrated that the effectiveness of a species as bait is not necessarily an indication of its suitability as food for rock lobsters.

The main diet fed during aquarium experiments was mussels and abalone, held alive in tanks until cut up for feeding. Small fish from local trawling were held frozen as an alternative food when needed. The general feeding procedure was to give a little more than would be eaten during one night and then to remove uneaten residues next morning.

The amount of food eaten each night varied with the size (age) of the animal and the temperature at which it was held. There was also a cyclic variation between moults. Feeding ceased two to six days before a moult and recommenced within two days after moulting, food intake then rising rapidly to a peak on the fourth or fifth day, thereafter declining slowly. For the two-year-old juvenile held at 26°C, the peak intake was 10 gm of food (abalone meat) in one night, while the mean intake over several successive moults was 2.7 gm per day per animal.

For optimum growth and survival, daily feeding was found to be necessary. When fed three times a week, the frequency of moulting was depressed significantly. When fed only once each week, not only was moulting much delayed, but also the animals did not gain much in size or weight when they eventually moulted. Whenever food was insufficient, rock lobsters began to attack and kill those helpless at the time of moulting.

Isolated rock lobsters have been held for many weeks without food though the quality of the product and the yield no doubt decline as muscle proteins are metabolised. Survival times in complete starvation depend on temperature, juveniles living for at least 24 weeks when held at 16°C but for little more than 14 weeks at 25°C.

Crowding: Western rock lobsters are generally gregarious. Not only does this have survival value against predators in the wild, but also the stimulus of living together in groups promotes feeding and growth rate (when food is plentiful). Juveniles held in isolation moulted far less frequently and so had a slower growth rate than crowded juveniles of the same age. Survival was not directly affected by crowding provided that each animal had sufficient food. Competition for food was alleviated by holding a single age group in each experiment.

Oxygen: Dissolved oxygen was normally kept as close as possible to saturation by maintaining a fairly rapid flow of sea water through tanks. Aeration by compressed air was added as a safeguard against any failure of the water circulation. No problems were experienced in this species with super-saturation of oxygen.

When dissolved oxygen fell to 60-67 per cent saturation, survival and moulting were not affected but the growth increment per moult was less, slowing down the overall rate of growth. Depression of oxygen levels to 47-55 per cent saturation resulted in deaths of most of those which were moulting.

Light cycle: As this species is generally a nocturnal feeder, it was thought that two regular periods of darkness every 24 hours might stimulate feeding and growth. However, an aquarium test showed no difference in growth rate between groups held under continuous light, those exposed to a 12-hour light-dark cycle, and those given a six-hour cycle. Rock lobsters held in continuous darkness actually grew significantly less than the other groups.

Dusk periods may be more effective than full darkness, but this aspect has not been tested as yet.

Shelter: When all other conditions were optimal, juveniles supplied with shelter had a higher rate of food intake and better growth than those deprived of shelter. Group shelters (made from PVC or asbestos-cement) were generally preferred to single shelters (sections of plastic or terracotta pipes).

Handling: Experience has shown that handling rock lobsters within two weeks prior to a moult tends to depress the growth increment at that moult. Handling newly-moulted animals should be avoided for two reasons. First, legs are much more likely to be shed at this stage (discussed below), and second, the soft-shelled animals are more prone to internal damage, resulting in lower food intake and depressed growth even when no limbs have been shed.

Limb loss: The western rock lobster autotomises limbs readily under conditions of stress or fright and also when extremities of limbs become caught inside the old shell during moulting. Missing limbs are replaced at the next moult. Loss of a large number of legs, or the repeated removal of only two or three legs, stimulated earlier moulting but the advantage of more frequent moulting was generally more than outweighed by the lower growth increment per moult, so that the overall growth rate was reduced as a result of limb loss.

Prospects for mass rearing juveniles

Final stage (puerulus) larvae brought into this laboratory have now been reared to adulthood (Figure 1), as described by Chittleborough (1974a). The practical problems of long-term rearing have been resolved and the optimum conditions are known.

If commercial rearing of juvenile western rock lobsters was to be carried out, the first problem would be the source of juveniles. The Western Australian regulation making it illegal to take rock lobsters of less than 76 mm carapace length is aimed at maintaining the level of recruitment into the fishery. Because of the relatively poor settlement of larvae in recent years on the southern portion of the coastal range of this population, protection of small juveniles must be maintained.

Towards the centre of the coastal range (approx. 29°S.), higher settlement of larvae has resulted from time to time in some of the shallow reefs being overcrowded, with competition for food and shelter limiting growth and survival. In such a situation, strictly limited cropping of young rock lobsters for rearing in capitivity might be carried out without reducing recruitment to the existing fishery. If juveniles aged two years were sought for pond rearing, selective fishing using traps with screened entrances would be necessary because of feeding dominance by larger (older) rock lobsters (Chittleborough 1974b). Such selective fishing would safeguard the survival of

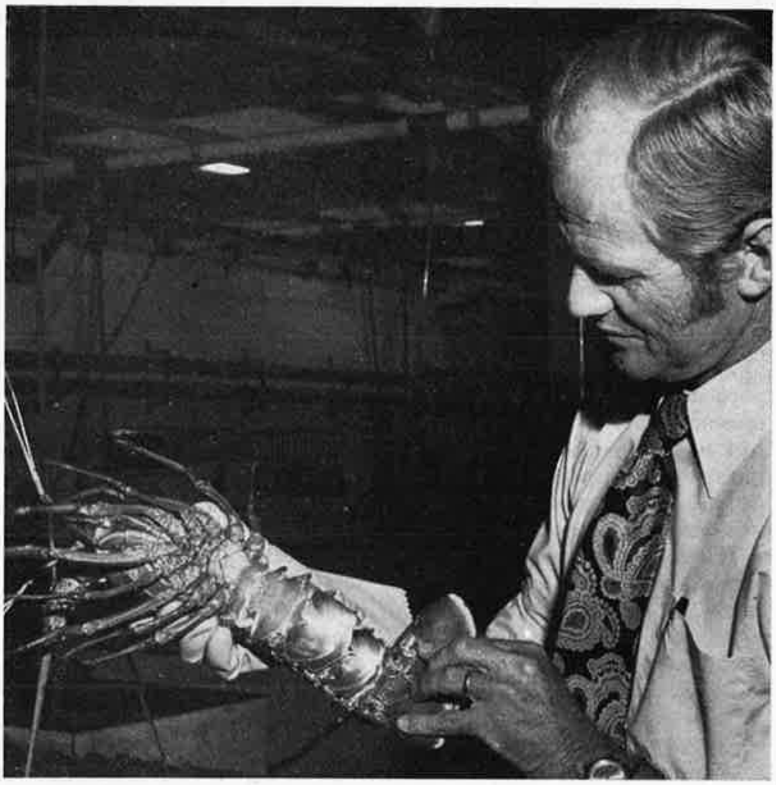
Dr. Chittleborough and laboratory assistant examine juveniles in a tank at the Waterman Laboratories. (Photo by Mike Brown, Australian Information Service, Perth).

older juveniles required to maintain recruitment to the fishery.

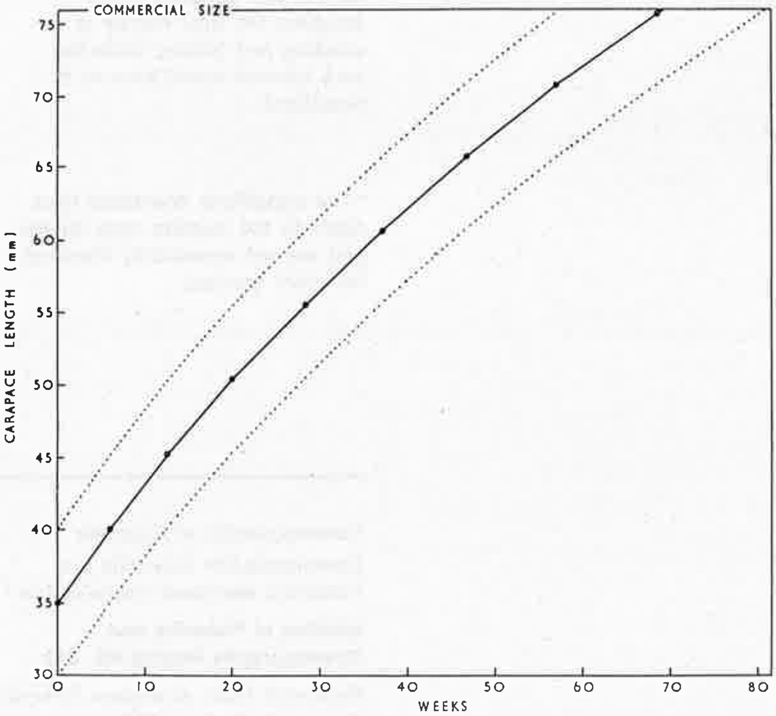
The next question is to what extent can the growth rate be accelerated under ideal conditions. Juveniles two years of age (carapace length 30-40 mm, mean 35 mm), can be raised to commercial size (carapace 76 mm) in 57-80 weeks (mean 68 weeks). In the wild population on reefs, those aged two years take 150-200 weeks to reach the legal minimum size (Chittleborough 1974a).

Under optimal conditions in tanks, survival of more than 95 per cent could be expected. In the open-circuit sea water system at this laboratory, infections were few, seldom lethal and not highly contagious. However in a small closed-circuit system set up in the University of Western Australia some years ago, there was one occasion when a fungal infection spread rapidly through the rock lobsters killing almost 50 per cent and leaving the remainder so weakened that feeding and growth were severely reduced.

If growth in mass rearing and survival was also high, the next question is how much food would be required. Feeding trials have achieved a mean gross conversion ratio of 3.6 for this species. This was measured with isolated individuals held at the optimum temperature (25°C); better conversion could be expected when held in groups as the juveniles are then stimulated to moult more frequently. This conversion ratio means that the feeding of 360 grams of wet flesh produces a gain of 100 grams of rock lobster total weight. Then to rear a two-year-old rock lobster (mean weight 42 gm) to legal size (mean weight 387 gm) would require a total food intake of 1240 gm over the period of some 68 weeks. A relatively cheap source of food would have to be found before this was an economical proposition.



Dr. Chittleborough displays six-year-old western rock lobster reared in an aquarium from a juvenile. (Photo by Mike Brown, Australian Information Service, Perth).



Growth achieved by juvenile western rock lobsters brought into aquaria at age two yrs. and held under optimum environmental conditions.

Trash fish from commercial trawling might be inexpensive although continuity of supply could be a difficulty. However rock lobsters have a strong preference towards molluscs and it remains to be verified whether a satisfactory growth rate can be achieved on a diet of scale-fish only. The mussel *Mytilus edulis* has proved satisfactory as a food for the western rock lobster and is common locally. If raft culture of mussels could be developed at a sufficiently low cost as in Spain (Ryther 1968), mussels could be converted to the higher priced rock lobster. If a food source was located some distance away from the rock lobster population, it might be more economical to move the two-year-old rock lobster (weighing 42 gm) rather than transport the 1.2 kg of food needed to grow this rock lobster to commercial size.

The need to maintain sea water temperature at a relatively high level (25°C) also presents problems. Two heat sources which might be economical are solar heat and waste heat from industry. Because of the high toxicity of copper to rock lobsters, conventional solar heaters canot be used. Heat absorbers of black plastic are available but those with narrow water passages could present problems of blockage by growths of marine fouling organisms.

The use of heat from industry is being investigated in other countries for aquaculture. In Cockburn Sound, close to the western rock lobster fishery, more than 12 million gallons of heated sea water is discharged every hour by industry, and the quantity is increasing (Chittleborough 1970). Apart from capital costs of equipment such as heat exchangers, this presents an economical method of maintaining juvenile rock lobsters close to the optimum temperature (25°C).

The quality of the product from pond raising rock lobsters needs to be considered. During aquarium experiments, the shells of rock lobsters held through several moults were generally paler than those from natural reefs, similar in appearance to the 'white' rock lobsters taken commercially in November and December each year. Taste panels at the end of aquarium experiments agreed that the product compared favourably with wild stock. In fact, the flesh of well fed, fast growing rock lobsters from the aquaria appeared to be more tender than that of the wild stock. Improved quality might be stressed if developing local restaurant trade featuring live hand-reared rock lobsters. A similar development in Japan has enabled live cultured prawns (for 'tempura') to attract a higher price than prawns taken by trawling, thus offsetting the cost of production (Ryther 1968).

Conclusions

There is no technical barrier to the mass rearing of juvenile rock lobsters. Under optimal environmental conditions*, the growth rate can be improved greatly, reducing the time taken by those aged two years to reach market size to a factor of 0.4 times that required by the wild stock. The total quantity of food required has been determined.

The real barriers are economic and legal. A potential pond farmer would first need to assess whether the capital outlay, maintenance and feeding costs could be offset by a market price acceptable to the consumer. If after making such an assessment, he was still attracted to the prospect, the legal barrier to catching and holding undersize rock lobsters would have to be negotiated.

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*The conditions described here apply to the western rock lobster and are not necessarily identical for other species.

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Environmental Factors Affecting Growth and Survival of Juvenile Western Rock Lobsters *Panulirus longipes** (Milne-Edwards)

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Abstract

The effects of temperature, photoperiod, oxygen, food supply, crowding, and autotomy of limbs have been measured under controlled conditions in aquaria. Growth rate increased with temperature to a maximum 26°C above which both growth rate and survival declined. Varying the length of photoperiod did not affect growth rate or survival, except that the growth rate was depressed significantly in continuous darkness. A mild deficiency of oxygen (60–67% saturation) resulted in a smaller size increment at a moult; depression to 47–55% saturation caused deaths at ecdysis. Daily feeding was necessary to maintain maximum rate of growth. The first response to decreased food supply was a reduction in frequency of moulting. More severe shortage of food also depressed growth increment per moult. Feeding rates and conversion ratios have been measured. Frequency of moulting (and hence growth rate) was depressed markedly when juveniles were held in isolation. At a moult replacing two lost limbs, the growth rate was not affected; replacement of four limbs reduced that moult increment. Single loss of up to four limbs did not result in an earlier moult, but repetitive loss of two or more limbs at or immediately after each ecdysis led to precocious moulting.

The impact of these and other components of the environment (shelter, salinity, turbidity, competitors and predators) upon juveniles during the 4 years spent on shallow coastal reefs is discussed. Food supply is emerging as the dominant factor determining growth and survival in the wild population.

Introduction

The western rock lobster is confined to the western coast of Australia from the vicinity of North West Cape down to Cape Naturaliste (Fig. 1). Within this range, juveniles spend 4–5 years concentrated mainly upon shallow reefs before moving out into deeper water towards the breeding stock. While resident on coastal reefs, juveniles remain within a relatively small home range (Chittleborough 1974*a*) with little dispersion unless displaced outside that range by fishermen.

In studying recruitment, it is necessary not only to measure the density and natural mortality of juveniles on these reefs (Chittleborough 1970), but also to understand the environmental pressures operating upon them to vary survival and/or growth. Measurements of growth and survival rates made at selected reef sites reflect the interaction of a variety of environmental factors. Before these interactions can be interpreted properly, the effect of each component of the environment should be measured separately under controlled conditions. The environmental factors selected for study in aquaria at the Western Australian Marine Research Laboratories were those considered likely to have impact mainly upon growth of the juveniles, although survival was also measured where possible.

* Described as a new species *P. cygnus* by George (1962), but relegated to subspecific status *P. longipes cygnus*, by Chittleborough and Thomas (1969).

It is proposed to discuss here all of the environmental factors likely to affect juvenile western rock lobsters during their period of residence on shallow coastal reefs, together with aquarium observations designed to assist in their evaluation.

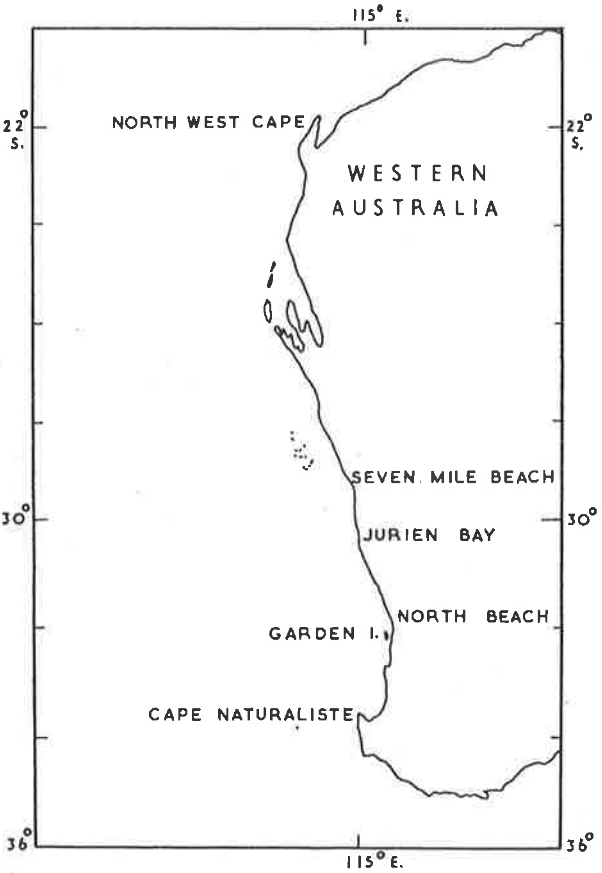


Fig. 1. Western coast of Australia showing locations mentioned in the text.

Methods

Areas of shallow (0–5 m) coastal reefs at Garden Island, Jurien Bay and Seven Mile Beach (see Fig. 1) have been set aside for research upon natural populations of juvenile western rock lobsters. Within these areas, juveniles have been regularly trapped and released after marking by spine clipping, tail punching or tagging (Chittleborough 1974*b*).

Samples from selected age groups of juveniles have been taken from these research areas and held in aquarium tanks under controlled environmental conditions. The seawater supply at the laboratory is an open-circuit system, the incoming seawater being pumped through sand-gravel filters of grain size down to 0·3 mm. As the laboratory is sited on an exposed part of the coastline some 22 km from the nearest estuary and its associated harbour and industry, the seawater is relatively uncontaminated by land run-off and pollutants. Temperature of incoming seawater ranged from 25·9° in summer to 14·9°C in winter. Corresponding salinities ranged from

36·7‰ to 34·8‰. Incoming seawater was generally close to full saturation with oxygen.

Size of individuals was recorded as carapace length measured (to 0·1 mm) mid-dorsally from the leading edge in front of and between the rostral horns (at the base of the eyes) to the rear of the carapace. Body weight of live animals was measured after removing free water by wrapping the rock lobster in a towel and swinging briskly in an arc 10 times (while supporting the animal between the hands). With practice, repeated weighings of an individual were within 0·5 g. Western rock lobsters were little affected by this treatment, provided that it was deferred for several days after a moult to enable the exoskeleton to harden. Exuviae were also weighed while wet but in this case, the limbs and tail were separated and each portion of the exuviae shaken to remove free water. The various segments of the old shell were then weighed together.

Table 1. Temperature (°C) of water pumped from adjacent reef through the seawater system of Western Australian Marine Research Laboratories

Year	Annual range	Annual mean	Summer mean (Dec.–Feb.)	Winter mean (June–Aug.)
1970	15·0–24·2	19·4	22·6	16·7
1971	15·3–25·6	19·5	22·7	17·1
1972	14·9–25·9	20·1	23·3	17·0
1973	15·6–25·4	19·5	22·5	16·9

Components of the Environment

Climatic Influences

Temperature

Amongst the shallow reefs of the research area at Garden Island, the water temperature ranged from a minimum of 15·9°C in winter to a maximum of 24·7°C in summer. The area was not visited sufficiently regularly to record the temperature cycle in detail, but temperatures related closely with those taken at the same time in the incoming seawater at the laboratory (Table 1) situated on the open coast 32 km north of Garden Island. Further north along the coast, water temperatures tended to be slightly higher. In the shallow research area at Seven Mile Beach, close to the centre of the coastal range of the western rock lobster, seawater temperature ranged from 15·8° to 27·6°C.

In order to measure the effect of temperature upon survival and growth, 32 reef-caught juvenile western rock lobsters, all 2 years of age, were divided into four groups of eight specimens, each group being held at a different temperature, i e. 20°, 23°, 26°, 29°C. Aquaria having a floor area of 2200 cm^2 and water depth of 30 cm each housed four animals. Compartmented shelters made of PVC were provided. Individuals in each aquarium were identified by marking the carapace with epoxy resin. All were fed daily with a slight excess of food (freshly cut mussels, abalone, or fish), the amount required being gauged when cleaning out the uneaten residue from the previous day.

The date of each moult was recorded, and after allowing the new exoskeleton to harden for a few days, the moulted animal was measured and re-marked, noting any loss of limbs. The date of any death was recorded. This experiment was commenced in January 1970 and terminated in February 1971, so that survival and growth at each of the four temperatures could be recorded throughout a full year.

Survival. As only eight individuals were held at each temperature, a precise measurement of survival rates could not be made. During the 12 months of the experiment, four deaths occurred at 29°C, two at 26°C, none died at 23°C, and two died at 20°C. Survival was apparently reduced at 29°C. Where death occurred it was usually at or immediately prior to ecdysis, which is similar to the observation by McLeese (1956) that lobsters (*Homarus americanus*) were less resistant to high temperatures at the time of ecdysis.

During preliminary tests of the temperature control unit, four other juvenile western rock lobsters (in the intermoult phase) acclimated to 29°C survived a 6 h exposure to 34°C.

Growth. In crustaceans, increase of size is a stepped process, length and weight increasing abruptly at each of a succession of moults. Therefore environmental factors affecting growth rate might operate upon the growth increment per moult and/or upon the frequency of ecdysis.

The increment (in carapace length) at the first moult after commencing an experiment was almost always less than at succeeding moults, due either to previous environmental conditions or to stress imposed when capturing and handling during the setting up of the experiment. The first moult increment was therefore not considered when comparing growth increments in these experiments. The size increment at a moult where more than two limbs were being replaced was also depressed (discussed below), so that these moult increments were also excluded. With careful handling, few limbs were autotomized during the experiment.

For these young western rock lobsters in their third year of life, the growth increment per moult did not differ significantly between the sexes. For example, at 23°C, the mean moult increment of females was $5\cdot04\pm0\cdot41$ mm and that of males was $4\cdot87\pm0\cdot24$ mm ($P > 0\cdot05$). Those held at a particular temperature showed no trend in growth increment per moult over several successive moults during the year, so that the data (with the exception of those noted above) could be pooled when comparing moult increments at different temperatures. In this experiment, the mean increment per moult tended to vary inversely with water temperature (Table 2), but variability was high. For those held at 20°C, the mean increment per moult was significantly greater than for those held at 29°C ($0\cdot05 > P > 0\cdot01$).

At a given temperature, the duration of the intermoult period did not differ significantly between the sexes (for well-fed juveniles in their third year of life). The duration of the intermoult period decreased as the temperature rose from 20°C to 26°C, then increased at 29°C (Table 2). Thus the frequency of moulting increased with temperature to a maximum of 26°C. However, at a particular temperature the duration of the intermoult period increased with successive moults throughout the year. This has been represented by linear regressions relating the duration of an intermoult (I days) to successive intermoult periods (p = 1–6).

$$
\begin{aligned}
&\text{At } 20^\circ\text{C}, && I_{20} = 62\cdot8 + 10\cdot9p \\
&23^\circ\text{C}, && I_{23} = 41\cdot6 + 7\cdot4p \\
&26^\circ\text{C}, && I_{26} = 35\cdot9 + 5\cdot3p \\
&29^\circ\text{C}, && I_{29} = 38\cdot6 + 8\cdot2p.
\end{aligned}
$$

By applying the mean increment per moult at a particular temperature (Table 2) to the corresponding regression given above, mean growth for those juveniles used in this experiment can be represented (Table 3). Those held at 26°C completed 6 moults in the year, while five moults occurred at both 23° and 29°C, and four moults at 20°C. Mean annual growth (in carapace length) was almost linearly related to temperature up to a peak close to 26°C, above which growth was depressed.

Table 2. Growth increment per moult and intervals between moults for western rock lobsters (aged 2+ yr) held at selected temperatures throughout 1970

	Water temperature			
	20°C	23°	26°	29°
	Moult increment (carapace)			
No. of moults	22	37	37	21
Increment range (mm)	3·7–7·6	2·4–6·3	3·0–6·7	2·7–6·5
Mean (mm)	5·10±0·40	4·96±0·24	4·74±0·28	4·63±0·43
	Mean duration of intermoult period (days)			
First intermoult	69·9	49·8	40·5	50·4
Second	87·1	54·3	46·7	53·2
Third	101·6	63·4	56·6	58·7
Fourth		74·1	51·7	69·0
Fifth		78·0	61·3	85·7
Sixth			70·8	

Table 3. Mean growth of juvenile rock lobsters aged 2+ yr held in aquaria at constant temperature for 1 year (excess food available)

Successive moult	20°C		23°C		26°C		29°C	
	Time (days)	Carapace (mm)	Time (days)	Carapace (mm)	Time (days)	Carapace (mm)	Time (days)	Carapace (mm)
	0	35·2	0	35·2	0	35·2	0	35·2
First	73·7	40·3	49·0	40·1	41·2	39·9	46·8	39·9
Second	158·3	45·4	105·4	45·1	87·7	44·6	101·8	44·4
Third	253·8	50·5	169·2	50·0	139·5	49·4	165·0	49·1
Fourth	360·2	55·6	240·4	55·0	196·6	54·1	236·4	53·7
Fifth			319·0	60·0	259·0	58·9	316·0	58·3
Sixth					326·7	63·6		
Annual growth		20·4		24·8		28·4		23·1

Growth of the same age group (2+ yr) remaining on the reefs in the Garden Island test area (from which the juveniles used in this experiment were obtained) was measured by the shift in modal length over the same 12 months. In the natural population, the growth increment over that year was 12·5 mm, far lower than that of the group in controlled environmental conditions held at the equivalent mean annual temperature (20°C group of Table 3). Other environmental factors superimposed in the natural population apparently restrict the growth rate in addition to temperature.

Light Cycle

The feeding behaviour of the western rock lobster appears to be similar to that of *Panulirus japonicus* (v. Siebold), which is a nocturnal forager having a bimodal feeding activity with peaks corresponding to dusk and pre-dawn (Kubo 1962). This feeding pattern continued for a time in a darkened room (Kubo and Masuda 1964). If prolonged exposure to another light cycle (e.g. two darkened periods of 6 h each day) could be used to establish a new feeding pattern, it might be possible to increase food intake and hence the growth rate.

Accordingly, 48 juvenile western rock lobsters, all aged 3+ years, were divided into four groups. One group was held under continuous light in a tank holding four animals in each of three compartments; another group was held similarly in a tank equipped to give 12 h alternating periods of dark and light; the third group was exposed to a cycle of 6 h of dark and light; while the fourth group was held under continuous darkness (apart from a red light of low intensity used for a few minutes when feeding and checking for moults). Individuals were identified using epoxy resin on the carapace, marks being replaced a few days after each moult. Shelter was not provided, as this would have shielded the animals. Transparent shelters were offered initially in case there was a thigmotactic response, but these shelters were ignored. All groups were fed daily with a slight excess of mussels, abalone, or fish.

Table 4. Growth (carapace) increments per moult for western rock lobsters aged 3+ yr held in aquaria under various light regimes

Light condition	No. of moults[A]	Moult increment (mm) Range	Moult increment (mm) Mean
Continuous light	32	2·7–7·0	4·75±0·29
12 hr light–dark	28	3·2–6·4	4·67±0·37
6 hr light–dark	32	2·9–6·6	4·54±0·32
Continuous dark	23	2·8–6·4	4·72±0·44

[A] Excluding first moult and moults replacing two or more limbs.

At the time of the experiment (1970), facilities were not available for heating the seawater, so that the water temperature in these tanks ranged from a maximum of 24·2°C in summer to a minimum of 15·0°C in winter. The experiment was maintained for just over 12 months so that growth could be compared throughout a full year.

The absence of temperature control increased variability of moulting frequency, making it difficult to compare groups, especially when the frequency of moulting was much reduced during winter. However, during the first 95 days of this experiment (before the temperature of incoming seawater had fallen to winter levels), the frequency of moulting did not differ significantly in the groups held under continuous light, 12 h light cycles, or 6 h cycles. For those held in continuous darkness, moulting frequency was significantly less than for those under the 12 h light cycles ($\chi^2 = 8\cdot57$, $0\cdot001 < P < 0\cdot01$).

The mean growth increment per moult did not differ significantly between the sexes nor did it vary seasonally, so the data from within a group could be pooled (apart from excluding the first moult after commencing the experiment, and moults replacing two or more limbs, as described earlier). Table 4 shows that the mean growth increment per moult did not vary significantly from one light regime to another.

Total growth through the whole year of the experiment (Table 5) did not differ significantly for those held under continuous light, 12 h light–dark cycles, or 6 h cycles. However, those held under continuous darkness grew significantly less ($0\cdot05 > P > 0\cdot01$) owing to some reduction in the frequency of moulting.

Since the western rock lobsters in this experiment were held at virtually the same sea temperature as those remaining in the test area at Garden Island, total annual growth of the same age group can be compared directly (Table 5). Marked individuals aged 3+ years at Garden Island grew significantly less than those held in aquaria under similar conditions of temperature and light. Other components of the environment of the natural population were again depressing growth rate.

From this experiment, it was concluded that varying day length did not enhance the growth of the western rock lobster. Growth was inhibited by continuous darkness; this is in direct contrast to the findings of Cobb (1970) for *Homarus americanus* and of Forster (1970) for *Palaemon serratus* that growth rates were increased in continuous darkness.

Table 5. Total growth in one year of juvenile rock lobsters aged 3+ yr exposed to different light periodicity, compared with those on natural reef

Light condition	No. of animals	Total carapace growth (mm) in one year Range	Mean
Continuous light	12	11·3–19·2	15·16±1·36
12 hr light–dark	12	7·9–19·4	14·10±1·87NS
6 hr light–dark	12	10·3–19·2	15·48±1·66NS
Continuous dark	12	7·9–17·6	12·41±1·70*
Garden Is. reef	10	8–18	11·4 ±1·8

* $0 \cdot 01 < P < 0 \cdot 05$. NS, $P > 0 \cdot 05$.

Oxygen

Living in shallow waters well mixed by wave and wind action and supported by photosynthesis of abundant algae and seagrasses, juvenile western rock lobsters would not be expected to experience serious deficiencies in oxygen. From the relatively few measurements taken in the study areas (during daylight), the dissolved oxygen concentration ranged from 76 to 115% saturation.

In aquarium experiments, dissolved oxygen concentration was normally kept as close as possible to full saturation. The effects of oxygen deficiency were not measured in separate experiments under controlled environmental conditions, but as an unplanned complication in other experiments. In an experiment varying the density of animals (described below), temporary restrictions at times in flow rate of heated seawater resulted in steeply falling oxygen gradients across compartmented tanks (e.g. from 104% saturation by the inlet to 47% at the outlet end of a tank).

Depression of oxygen levels to 47–55% saturation did not affect survival or feeding activity of animals in intermoult phase and did not appear to delay moulting. However, at ecdysis there was a much increased risk of death, and those surviving had a depressed growth increment at moult, as shown in Table 6. McLeese (1956) noted that the lobster *Homarus americanus* was less resistant to low oxygen concentration when moulting.

Aquarium held animals exposed to oxygen levels of 60–67% saturation while moulting survived, but the growth increment per moult was depressed. Thus a mild deficiency of oxygen at the time of ecdysis results in a slower rate of growth of juvenile rock lobsters.

Salinity

Within the shallow reef areas under study, salinity ranged from 34·4‰ following winter rains to an occasional peak of 37·7‰ with high evaporation during summer.

Dall (1974) measured the tolerance of juvenile western rock lobsters to changes of salinity. Because of the relatively wide tolerance observed (25–45‰) compared with the small variability in salinity experienced in the natural population, no experiments were carried out under controlled environmental conditions to examine possible effects on growth rate of varying salinity.

Table 6. Moult increments and deaths in groups of rock lobsters aged 3 yr held at 25°C for 1 year at four successive distances from water inflow (oxygen supply)

Position in tank	No. of animals	Total no. of moults[A]	Growth increment per moult (mm)[A]		Deaths	
			Range	Mean	No.	(%)
(1) Water inflow	17	46	3·0–7·4	4·92±0·25	1	5·9
(2)	18	59	2·2–6·6	4·00±0·27	2	11·1
(3)	21	68	0·8–6·5	3·95±0·27	2	9·5
(4) Water outlet	7	10	0·6–4·6	2·73±0·84	5	71·4

[A] Excluding first moult.

Turbulence

The more exposed of the shallow coastal reefs are frequently subjected to strong wave action. Western rock lobsters are well adapted to such conditions and have been observed foraging at night over reefs within the surf zone. Severe storms could cause some mortality of juveniles if rocks were dislodged. On the other hand, storm action might improve the food supply by dislodging or killing individuals of other species. Fishermen claim that catch rates decline during periods of very calm weather and improve immediately after a storm, suggesting that turbulent conditions stimulate feeding activity.

Although there may be some effects on survival and growth, this component is probably a random variable in the environment and of less importance than other factors.

Turbidity

This may be linked with turbulence, but in addition some portions of the coastline may have finer material which stays in suspension longer. For example, within the research area at Seven Mile Beach, underwater visibility is restricted to a few centimetres at times. This could have survival value against predators relying upon vision to locate prey.

Measurements of turbidity have not yet been made in the various research areas along this coast.

Resources

Food

Although a detailed study has not yet been made of food and feeding on the reefs, experiments in aquaria have given some indication of the food preferences of this species. Like the southern rock lobster (Fielder 1965), the western rock lobster prefers molluscs and fish rather than mammalian flesh, and fresh food is preferred rather than stale. Western rock lobsters held in aquaria fed readily on abalone (*Haliotis roei*), mussels (*Mytilus edulis planulatus*), and *Octopus* sp. flesh, various teleosts, crabs (*Plagusia chabrus*), and less readily on sea urchins (*Heliocidaris* sp.). The main diet fed during aquarium experiments was abalone and mussels, held alive in separate tanks at the laboratory until cut up for feeding. Small teleosts from local trawling were held frozen to supplement the diet when needed.

To test for preference towards either fish or abalone, 12 aquaria each holding four juvenile western rock lobsters were supplied daily with weighed quantities of fish and abalone in equal numbers of pieces. Uneaten pieces were removed next day, drained and weighed. Over three nights, the 48 rock lobsters consumed a total of 401 g of abalone muscle and 87 g of fish (i.e. a ratio of 4·6:1). In spite of such a preference for abalone, fish flesh is highly effective as bait in rock lobster pots.

In examining other prospects for an economical source of food for captive western rock lobsters, a feeding trial was carried out offering as a food the banded blowfish *Sphaeroides pleurogramma* (Regan), a pest species prevalent in the region at present. Ten juvenile western rock lobsters, all 3+ years of age, were divided into two groups of five, one group being fed pieces of blowfish daily, while the control group was given mussels and abalone. Details of survival and growth of each animal were recorded.

When first offered pieces of blowfish, the rock lobsters accepted eagerly, as had been observed on other occasions when the diet was varied. However, they quickly lost interest in blowfish and refused to eat it. Moulting was delayed, growth increments at moult were depressed below those of the controls, and two animals died. After the experiment had continued for 23 weeks, analysis of gastric fluid taken from the three surviving rock lobsters indicated that they were in extreme starvation (Dall, personal communication). The survivors were then placed back on the normal diet of mussels and abalone but recovery was slow, one dying 4 weeks later.

Although reef-dwelling western rock lobsters can be trapped using blowfish as bait, it is evident that they reject this species as a regular food, to the point of starving to death. Thus neither the effectiveness of a bait nor the initial response of a rock lobster in a feeding trial can be used as an index of the acceptability of a given species as a food for rock lobsters.

It was not known whether well-fed western rock lobsters forage each night or whether satiation is followed by a period of inactivity. Also it was not known whether a food shortage affects growth primarily through the frequency of moulting or the growth increment per moult. To answer these questions, 30 juveniles aged 2+ years were held in groups of five animals per tank at a constant temperature of 25°C. Individuals were identified by tail punching so that growth and survival of each could be recorded. Ten of these young western rock lobsters were fed daily with a slight excess of food, uneaten residues being removed next morning. Ten were given excess food three times per week, while the remaining 10 were fed only once per week. The experiment was maintained for 6 months.

It was quickly evident that feeding occurred each night despite satiation the previous night, the food intake of the group fed excess daily being maintained with minor fluctuations as individuals within the group moulted. Those offered excess food less frequently could therefore be expected to experience a food shortage.

The mean growth increment per moult (excluding the first moult, as explained earlier) of those fed three times per week did not differ significantly from that of those fed daily (Table 7). Of those fed once each week, the growth increment per moult was depressed significantly ($P < 0 \cdot 001$). Table 7 shows that in those fed three times per week, the frequency of moulting was reduced, the intermoult period being significantly longer than that of those fed daily ($0 \cdot 05 > P > 0 \cdot 01$). Those fed only once per week showed considerable lengthening of the intermoult period ($P < 0 \cdot 001$).

In this experiment, a shortage of food also affected survival, some individuals being attacked and killed during or immediately after moulting. In most instances only a small quantity of the victim was actually consumed. Fresh animals of the same age group were added to maintain a constant density. During the 6 months, no deaths occurred amongst those fed daily, one death occurred amongst those fed three times each week, while seven deaths occurred amongst those fed only once per week.

Table 7. Growth per moult and intervals between moults for groups of 10 juveniles (aged 2+ yr) held at 25°C for 6 months under various rates of feeding

			Excess food fed		
	Daily		3 days per wk		1 day per wk
			Moult increment (carapace)		
No. of moults	29		22		11
Increment range (mm)	3·6–6·1		3·4–6·6		1·2–5·6
Mean (mm)	5·15±0·25	NS	5·24±0·34	***	3·78±0·75
			Mean duration of intermoult period (days)		
1st intermoult	42·0	*	50·7	***	79·0
2nd intermoult	47·7		59·2		84·5

NS $P > 0 \cdot 05$. * $0 \cdot 01 < P < 0 \cdot 05$. *** $P < 0 \cdot 001$.

These results show that the first effect of a mild shortage of food is a decreased frequency of moulting. At a more severe shortage of food, not only is moulting delayed further, but also the growth increment at moulting is depressed and mortality increased by intraspecific aggression.

In a survival test, seven juveniles aged 2+ years were isolated in separate aquaria and, after feeding excess food daily for 1 week, were held in complete starvation. Temperature was not controlled in this case, being at the ambient sea temperature (23·5°C initially, falling to 16·3°C during the next 6 months). Two animals which were close to moulting at the commencement of the test succeeded in moulting, after which no further moults occurred. The first death occurred during the 24th week of starvation. One animal remained alive after 43 weeks.

Food intake. The quantity of food eaten was determined by holding juvenile western rock lobsters in isolation, supplying a weighed piece of abalone foot muscle each day, and weighing the uneaten residue remaining next morning (after draining on absorbent paper). As well as being a favoured food, abalone muscle did not fragment easily, making weighings more reliable than would be possible with other food.

Fig. 2 shows typical feeding patterns of two individual juvenile rock lobsters aged 2+ years offered excess food daily. The longer interval between moults for an individual held below the optimum temperature (discussed earlier) is evident. Feeding recommenced within 2 days of moulting, food intake rising rapidly to a peak on the fourth or fifth day. Thereafter, the daily food intake followed a downward trend though fluctuating very considerably. After an initial period of intense feeding, those held at the lower temperature did not feed every day (Fig. 2), but there was not a regular pattern of feeding activity. Feeding ceased 2–6 days before the next moult.

Owing to the pattern of variation in amount of food eaten each day, it is difficult to compare feeding rates at different water temperatures. However, if the mean daily intake of food throughout each intermoult period is compared, the feeding rate for 2-year-old juveniles held at 26°C ($2\cdot67 \pm 0\cdot20$ g per day) was significantly higher than at 23°C ($2\cdot06 \pm 0\cdot20$ g per day) ($P < 0\cdot001$).

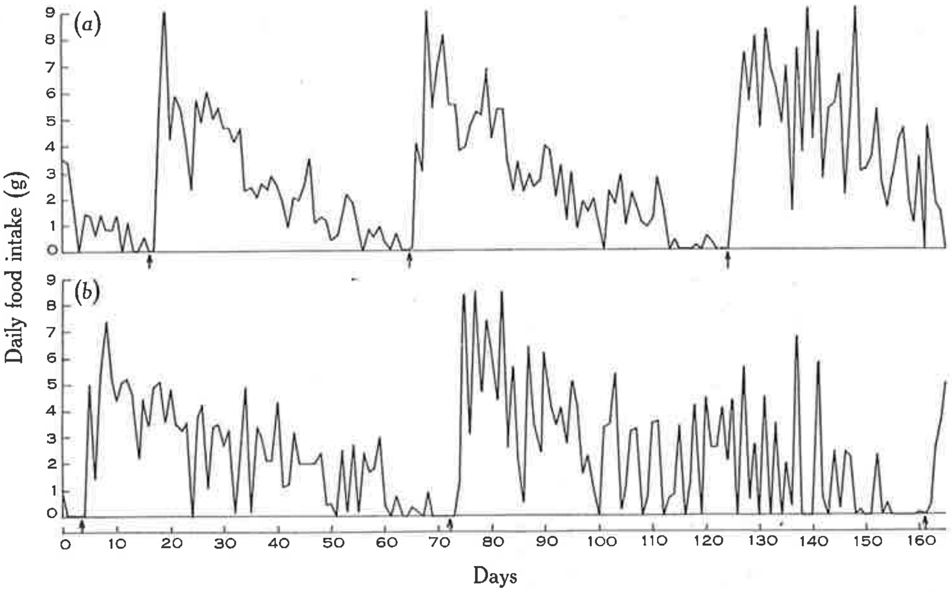


Fig. 2. Daily food intake of two juvenile rock lobsters aged 2+ years, through successive moults (arrowed): (*a*) specimen held in aquarium at constant 26°C; (*b*) specimen held at 23°C.

Food conversion. In order to assess the efficiency of conversion of food to body tissue, the relation between weight of food eaten in a given period and the corresponding gain in body weight should be measured. The body weight of a rock lobster increases in a series of steps with rapid intake of water at each ecdysis. During an intermoult period, tissue growth replaces water taken up at the previous moult. If it is assumed that an individual does not moult again until the water taken up at the previous moult is replaced by tissue growth, then the ratio of total food eaten during an intermoult period to the total water uptake at the moult prior to that period gives a measure of the efficiency of food conversion.

Total water uptake at a moult was taken as the difference in live body weight before and after moulting, plus the weight of the exuviae. Animals were weighed several days after moulting in order to avoid internal damage and limb loss which can result if handled while soft shelled. Despite careful handling, it was often observed that on the night following weighing an animal, food consumption was temporarily depressed.

Fig. 3 shows the relation between water uptake at moult and total food consumed at intermoult for juvenile western rock lobsters aged 2+ years held in isolation at constant temperatures of either 26°C or 23°C and fed daily with abalone foot muscle. Linear regressions were considered sufficient to represent relationships for these individuals. Extrapolation to older or younger animals may be unreliable, Gerking (1962) having shown that the efficiency of food conversion declined with age in the bluegill sunfish.

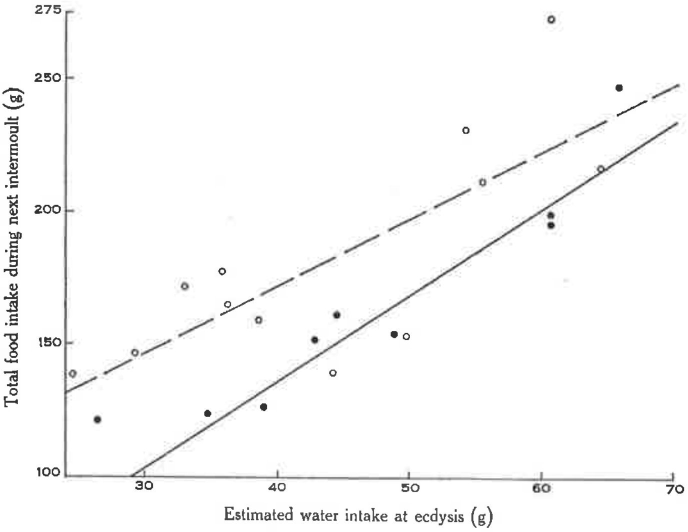


Fig. 3. Relation between water uptake at moult and total food consumed at subsequent intermoult, for western rock lobsters aged 2+ years. Held at 26°C (●) and 23°C (○).

Using the total food consumed during an intermoult period and the total water uptake at the moult initiating that period as an index of food conversion, Fig. 3 indicates that the overall conversion in western rock lobsters differs with water temperature. The regressions for each of the temperatures did not differ significantly in slope but their positions differed significantly ($P < 0 \cdot 05$), so that the intercept for those held at 23°C was higher than that of those held at 26°C. If the intercept was taken as representing the maintenance requirement for food (as applied by Allen (1951) in the case of trout), the results summarized in Fig. 3 would appear to indicate a higher maintenance requirement for rock lobsters held at the lower temperature, apparently in contradiction to metabolic rate increasing with temperature.

However, these data are for full intermoult periods, and as shown previously (Table 2) the intermoult periods at 23°C are longer than at 26°C. When the total food intake and the gain in body weight (as estimated from water uptake at moult) were both divided by the duration of the intermoult period, the resultant data (Fig. 4) for individuals held at 23°C and 26°C did not differ significantly in either slope or position of regression. On this basis there is no difference in conversion ratio of food to body tissue in juvenile rock lobsters at the two temperatures tested, except for the indirect effect of the lower temperature delaying moulting and so increasing the total amount of food utilized for maintenance requirements.

For the data shown in Fig. 4 the relation between mean daily food intake (f) and estimated growth in flesh weight gained per day (w) was

$$f = 1 \cdot 035 + 2 \cdot 096w$$

with a correlation coefficient of 0·866. The slope of this regression (2·096) is then an estimate of the net conversion ratio for the conversion of food to additional body tissues by juvenile western rock lobsters in their third year of life when held under these conditions.

For practical purposes in estimating the total food requirements of western rock lobsters the gross conversion ratio is needed. Using the data shown in Fig. 3 for the temperature of 26°C, the mean gross conversion ratio for rock lobsters aged 2+ years held at near-optimum conditions was $3\cdot57 \pm 0\cdot30$. This value combines requirements for maintenance as well as growth.

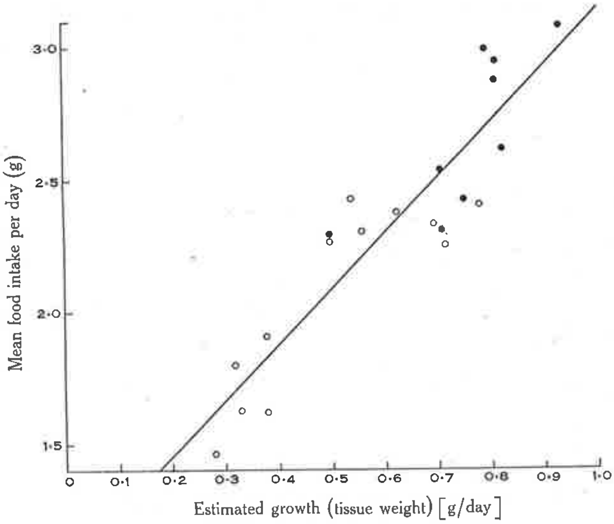


Fig. 4. Relation between mean daily food intake and estimated growth in tissue weight per day for western rock lobsters aged 2+ years. Held at 26°C (●) and 23°C (○).

Shelter

Unless storm action breaks part of the reef or removes sediment to expose more rock, the total quantity of shelter present on a given reef is virtually constant. However, the amount of shelter available to rock lobsters may vary from time to time if a portion of the total shelter is occupied by predators or competitors. Evidence for this came from the Garden Island research area. On a reef which was marked out with numbered trap sites, there were occasions when octopus took up residence near a particular site. Western rock lobsters were rarely present in shelter adjacent to a hole occupied by an octopus. When diving to hand-set traps on numbered sites, it was sometimes found that an octopus had already left its shelter and entered a trap. The octopus was removed, killed and placed in the boat and the trap still set on that site. On such occasions, the trap seldom took rock lobsters, but they could be captured at that site when trapping a month later. This indicates that on relatively uncrowded reefs, the presence of other species such as octopus reduces the amount of shelter available to rock lobsters.

Members of the Same Species

Chittleborough (1970) showed that in reef populations, natural mortality increased with density of juvenile western rock lobsters. Increased aggression resulting from a shortage of shelter and possibly food supply were suggested as factors responsible for this. An aquarium experiment carried out during 1969 was cited as evidence that mortality increased with density despite an excess of food being supplied. However, in that experiment, food (in excess) was given only twice per week. A subsequent experiment (see Table 7) showed that the earlier feeding regime had been inadequate.

Another experiment designed to measure the effects of crowding under conditions of constant (optimum) temperature and excess food supply was carried out in aquaria during 1971. Juveniles aged 3+ years were held in compartments of equal area (4140 cm^2), either singly or in groups of four, eight, or 16 animals. Incoming seawater was maintained at 25°C. All were fed daily with a slight excess of mussels, abalone or fish, uneaten residues being removed the following morning. Details of moulting, growth and survival were recorded for each individual.

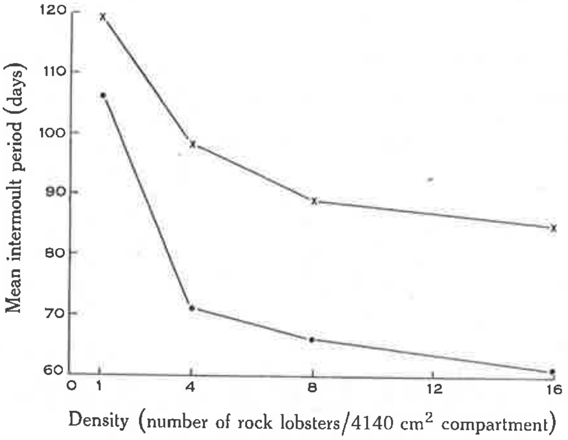


Fig. 5. Crowding experiment: relation between intermoult period and density of rock lobsters. First intermoult period (●). Second intermoult period (×).

The increased mortality under crowded conditions recorded in the earlier experiment did not occur when a daily feeding pattern was maintained, indicating that the previously recorded mortality had been due to lack of food rather than to behavioural stress imposed by crowding. Growth increment per moult was not affected by crowding while food supply was in excess. However, frequency of moulting was affected markedly by crowding, those held in isolation experiencing particularly long intermoult periods (Fig. 5), despite the fact that the perforated partitions separating compartments allowed some degree of contact between an individual and an adjoining group. This result is in direct contrast to the response of the land crab *Gecarcinus* which has a shortening of the intermoult period when isolated (Skinner and Graham 1972).

Members of Other Species

Other species constitute an important part of the rock lobster's environment if they compete for a share of a resource or constitute a threat to survival (by predation or disease). As a full study had not been made of these aspects, only general observations can be noted here.

The possible role of octopus as a competitor for shelter on reefs has been discussed earlier. Various species of fish and crabs compete with rock lobsters for food. On some of the more exposed reefs, the frequency with which the crab *Plagusia chabrus* is taken in rock lobster traps indicates that this species may compete strongly for food.

Western rock lobsters have been observed to eat dead *P. chabrus*, but were unable to capture live (fully grown) individuals in aquaria.

The octopus is regarded by fishermen as a serious predator upon rock lobsters. While it is undeniable that an octopus within a rock lobster pot will often kill and eat a western rock lobster and cause others to autotomize legs, it is not clear whether the octopus was initially attracted to the pot by the bait or by the captive rock lobsters. Western rock lobsters dropped back on to a reef after tagging have at times been observed to be taken by an octopus, but here again the rock lobsters were under conditions of stress.

On one occasion the author observed an encounter between an octopus and western rock lobsters under natural conditions on a reef. As the octopus swam past the sheltered hollow containing several juvenile western rock lobsters, the latter moved forward in the aggressive posture, antennae directed towards the octopus, which paused and then continued along the reef face. Levels of predation by octopus on undisturbed populations of western rock lobsters remain undetermined.

Various fish such as the bald-chin groper (*Choerodon paynei*), westralian jewfish (*Glaucosoma hebraicum*), snapper (*Chrysophrys unicolor*), and the whiskery shark (*Furgaleus ventralis*), have been reported as predators upon the western rock lobster. The wobbegong or carpet shark (*Orectolobus ornatus*) is plentiful on coastal reefs and is often caught in rock lobster traps. Examination of stomach contents did not reveal any remains of western rock lobsters but showed that the wobbegong includes octopus in its diet so its position in the food chain may favour the survival of rock lobsters.

Man has become part of the environment of the juvenile western rock lobster as fishermen examine the catch taken in rock lobster pots, freeing those which are below the legal size. Some of these are released away from the reef of capture. The effect of such displacement away from the home range of an individual has been discussed by Chittleborough (1974*a*). Handling may also result in loss of limbs: the effects of this are discussed below.

Hazards

This term is applied in the strictly limited sense used by Browning (1963) to factors which influence an animal's chances of survival and reproduction and yet are neither resources nor extensions of another animal's activities.

Moulting is one such hazard for the western rock lobster. This does not refer to the increased risk of attack by underfed western rock lobsters or by other predators to which a rock lobster is more vulnerable during ecdysis and until the new shell has hardened. Irrespective of all other components of its environment, each moult represents a hazard for the western rock lobster. Any delay in freeing itself from the exuviae during ecdysis means that the rapid intake of water at that time may result in the animal being trapped in the partly shed exuviae and dying.

In aquaria it has been observed that when a moulting western rock lobster has difficulty in freeing a limb from that part of the exuviae, the limb is quickly autotomized, thus ensuring rapid escape from the old shell during the critical phase of water uptake and swelling of the body to the new size. During a difficult moult an animal may shed several legs in this way.

Autotomy of limbs has generally been regarded as having its main survival value in escaping from predators. However, in the case of the western rock lobster, selection towards such an adaptation may have come through the repeated hazard of moulting.

Having survived a difficult moult by shedding several legs, a western rock lobster may then be less able to compete for food or to escape from predators. The same applies to animals which autotomized limbs while escaping from a predator or when handled by fishermen before being rejected as undersized, but these are extensions of the effects of other species in the western rock lobster's environment.

There remains the question of the effect of limb loss upon subsequent growth. In some species of the Brachyura, autotomy of limbs induces precocious moulting. Skinner and Graham (1972) found that loss of at least five legs was required in order to shorten the intermoult period of crabs.

In an experiment aimed at measuring the effect of limb loss on growth of western rock lobsters, three groups of eight juveniles, all aged 2+ years, were held in aquaria at 25°C and fed excess food daily. Individuals were identified by tail punching. In one group, two legs were removed from each individual within a few days after each moult. Pinching of a leg between the fingers resulted in its autotomy within seconds. A different pair of legs was removed on successive occasions. In the second group, four legs were removed after each moult, while those in the third group were maintained intact as controls. Missing legs were always replaced at the following moult, even when removed 28 days after ecdysis. (In that instance, the next moult occurred 41 days after removing the legs.)

Table 8. Effects on growth of the regular removal of limbs from western rock lobsters aged 2+ yr held in groups at 25°C and fed excess daily

	Controls (intact)	2 legs removed after each moult	4 legs removed after each moult
	Growth (carapace) increment		
No. of animals	8	5	8
Total no. moults	29[A]	15[B]	37[A]
Range (mm)	2·8–6·3	3·0–6·1	1·6–5·1
Mean (mm)	4·62±0·25	4·57±0·49	3·76±0·19
	Duration of intermoult period (days)		
1st intermoult			
Range	31–47	—	33–40
Mean	39·6±4·4	—	37·0±1·8
2nd intermoult			
Range	38–85	37–45	37–54
Mean	56·8±11·2	40·0±3·1	42·8±4·6
3rd intermoult			
Range	48–104	42–51	36–58
Mean	64·0±14·6	45·4±3·1	44·5±4·7
4th intermoult			
Range	54–88	51–67	45–65
Mean	70·3±12·7	57·2±5·9	53·4±4·3

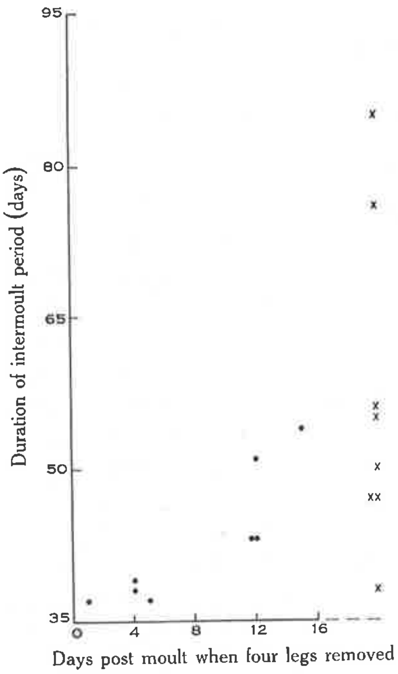
[A] Excluding first moult. [B] Excluding first and second moults.

Failure of water circulation one night resulted in deaths of five of the group with two legs removed and depressed the growth increment at the next moult of the three survivors of that group. As only two replacements were available the experiment was continued with five animals in the group.

Growth of the western rock lobsters in the three groups, over the 9 months that the experiment was maintained, is summarized in Table 8. As there was no difference in growth increment per moult between the sexes and no trend with time over this period, all moult increments from a particular group of animals were pooled. Mean increment per moult of those regenerating two legs did not differ significantly from that of the controls. However, replacement of four legs resulted in a significant decrease in the mean growth increment per moult ($P < 0 \cdot 001$).

Table 8 shows that mean intermoult periods in the groups having two or four legs removed regularly were shorter than corresponding mean intermoult periods of the intact controls. Because of the small number of animals remaining in the group having two legs removed, the mean durations of corresponding intermoult periods were barely significantly different (at the 5% level) from those of the controls. For those with four legs removed, the mean duration of the first intermoult period did not differ significantly from that of the controls, but the means of all subsequent intermoult periods during the experiment were significantly shortened ($P < 0 \cdot 05$).

Fig. 6. Duration of second intermoult period for rock lobsters having had four legs removed at varying times after moulting (●), compared with intact controls (×).



As shown in Fig. 6, the shortening of the intermoult period was most marked if leg removal took place within 1 week of moulting. Hence the trends towards shortening the intermoult period would have been accentuated if, in every instance, the legs had been removed immediately after ecdysis.

In summary, these results show that while a single loss of four legs did not stimulate a juvenile western rock lobster to an earlier moult, the growth increment at that moult was depressed. Repeated loss of even two legs led to precocious moulting. The overall effect of regular removal of two legs from well-fed juvenile western rock lobsters within a week after each moult would be a slight overall increase in growth rate, due to the stimulus to higher frequency of moulting with no suppression of the growth increment per moult. However, regular removal of four legs would result in an overall decrease in growth rate since the higher frequency of moulting is accompanied by a lower growth increment per moult.

Discussion

While the prime purpose of the experiments carried out in aquaria under controlled environmental conditions was to understand better the ecology of juvenile western rock lobsters on shallow coastal reefs, measurement of the effects of separate components of the environment on growth and survival have enabled an assessment to be made of the prospects for mass rearing juveniles in captivity (Chittleborough 1974*c*). When held at the optimum temperature of 26°C, each juvenile aged 2+ years requires a mean of 2·67 g of food (as abalone muscle) per day. The consumption of 3·57 kg of that food by such a group could result in a total gain in weight of 1 kg in body tissue. In practice the gross conversion rate within a group might be better than this, since the intermoult period decreases with crowding (Fig. 5), thus reducing the proportion of food required for maintenance activity.

Within the reef populations, the various components of the environment operate together to influence the growth and survival of young western rock lobsters.

Of the climatic factors, temperature has the greatest importance. The optimum temperature for growth and survival is 25–26°C, considerably above the mean annual temperature of inshore waters inhabited by these juveniles. Chittleborough (1974*d*) has also shown that when held at 25°C, adult western rock lobsters undergo repetitive breeding throughout the year, suggesting that this may reflect recent evolution from a tropical stock.

Although temperature is an important factor in determining growth rate under otherwise favourable conditions, reef dwelling juveniles often do not achieve the growth rate predicted for the mean water temperature at a given location. Other environmental factor(s) are superimposed to limit growth on the shallow reefs.

Most of the environmental factors affecting growth operated upon the frequency of moulting rather than on the growth increment per moult. Two separate conditions were found to depress the increment at moulting: a mild deficiency of oxygen (60–67% saturation), which was not associated with any delay in moulting nor with increased mortality; and a severe shortage of food, which was accompanied by less frequent moulting and increased mortality due to intraspecific aggression.

Food supply is emerging as a major determinant of both growth and survival of juvenile western rock lobsters in natural populations. This conclusion is based at present upon indirect evidence of the results of aquarium experiments described, plus field observations of density dependent mortality (Chittleborough 1970) and measurements of growth rates (to be published separately).

Shortage of food may be relative or absolute. A relative shortage would arise if, because of their behaviour patterns, some juvenile western rock lobsters did not obtain sufficient food even though the resource was still available in the area. Food (mainly molluscan) is present in the reefs and also on the adjacent seagrasses. Some rock lobsters forage in the seagrass beds at night, returning to the shelter of the reefs by dawn. If the area of seagrasses is large in relation to the shelter available, food on the more distant portions of the seagrass beds will be inaccessible to the western rock lobsters. A relative shortage of food might arise even on an uncrowded reef. Because of their gregarious behaviour and limited home range, some members of a group of rock lobsters may not obtain sufficient food within their segment of reef.

An absolute shortage of food for rock lobsters on a reef might be due to (i) a decline in the density of food species (for reasons other than predation), (ii) interspecific competition for a limited food supply, or (iii) intraspecific competition for food. The levels of the three separate variables involved here (density of food species, density of competitors, and density of juvenile rock lobsters) might each be determined by different environmental factors. For example, recruitment within the food species might be determined by localized climatic factors on or adjacent to the reef, whereas recruitment to the juvenile western rock lobster population (settlement of puerulus larvae) may be determined by oceanic conditions some hundreds of kilometres away (Chittleborough and Thomas 1969). Measurements of the density of food species and also of competitors are required before these interactions can be discussed further.

Crowding is likely to produce~~d~~ an absolute food shortage, the resulting increased intraspecific aggression being one cause of density dependent mortality recorded on these reefs. The role of predators and competitors in contributing to increased mortality at higher densities of western rock lobsters needs further investigation.

The impact of a food shortage depends to some extent upon the age composition of the population of juvenile western rock lobsters present on a reef. If the youngest of the four age groups present was from a relatively poor year class in relation to the others, its members might be expected to have lower growth and survival rates than if the older age groups were less well represented. This may be part of the reason why the growth of those aged 2+ years present on the reefs at Garden Island during 1970 was less than those of the same age taken from that research area and held at an equivalent mean temperature in aquaria (see above).

Irrespective of all other components of the environment, moulting represents a hazard to both survival and growth of western rock lobsters, especially for juveniles as these moult more frequently than adults. Autotomy is suggested primarily as an adaptation for survival when limbs are caught within the exuviae during ecdysis. Having survived such a moult, the replacement of more than two legs at the succeeding moult resulted in a depression of the growth increment. While a single loss of four legs did not stimulate a juvenile to an earlier moult, repeated loss of even two legs led to precocious moulting.

Acknowledgments

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Fluctuations of Year-class Strength and Recruitment in the Western Rock Lobster *Panulirus longipes** (Milne-Edwards)

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Abstract

Settlement of puerulus larvae on collectors composed of artificial seaweed and measurements of density of young juveniles on 'nursery' reefs show wide fluctuations in year-class strength, recent settlement from the spawning crop of 1973–74 being particularly high.

Owing to restricted holding capacity of the shallow 'nursery' reefs (mainly due to limited food supply), density-dependent mortality reduces most year-class strengths to similar levels by the time juveniles reach 5 years of age. Particularly weak year-classes have been shown to be associated with poor catches from the coastal 'white' fishery at the opening of a fishing season. The applications of these findings to the management of the fishery are discussed.

In theory, part of the wastage resulting from excess settlement of larvae in certain areas might be saved by transplanting to less crowded reefs or by mass-rearing in ponds, without diminishing recruitment from those left on the now overstocked reefs.

Introduction

The western rock lobster is confined to the western coast of Australia, from approximately North West Cape to Cape Naturaliste (Fig. 1). The majority of the commercial catch is taken between 28 and 32°S. (Sheard 1962).

After a planktonic life of 9–11 months (Chittleborough and Thomas 1969) the surviving larvae (puerulus stage) settle in shallow coastal areas. The younger juveniles concentrate on shallow limestone reefs (to depths of 10 m, with some larger juveniles to 20 m) while adults are generally confined to deeper water (30–150 m).

Each juvenile has a relatively small home range (Chittleborough 1974*a*), remaining on the one segment of shallow reef for several successive years. Migration to deeper waters usually takes place at 5–6 years of age, though the recovery in January 1975 of a juvenile tagged on that reef in January 1970 shows that 'nursery' reefs may contain a few individuals of 7 years of age.

Phillips (1972) showed that the last larval stage, the puerulus, could be captured using collectors composed of artificial seaweed moored at the surface within the protection of the coastal reefs. Chittleborough (1970) has measured the densities of juvenile populations on test reefs adjacent to these collectors.

In this paper the relative densities of larval settlement at selected sites, as recorded from the collectors, are compared with the subsequent densities of juveniles on adjacent reefs. The relation between these densities and subsequent recruitment to the commercial fishery is examined.

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* Described as a new species, *P. cygnus*, by George (1962) but relegated to subspecific status by Chittleborough and Thomas (1969).

Methods

Larval Settlement

Collectors composed of artificial seaweed (Phillips 1972) were used to sample the puerulus larvae at the time of settlement. Six collectors have been maintained since July 1968 at Seven Mile Beach. From June 1969 three collectors have been operating at Garden Island and five at Jurien Bay (Fig. 1). At each locality collectors were moored up to several hundreds of metres apart in order to check for localized differences in larval distribution during settlement.

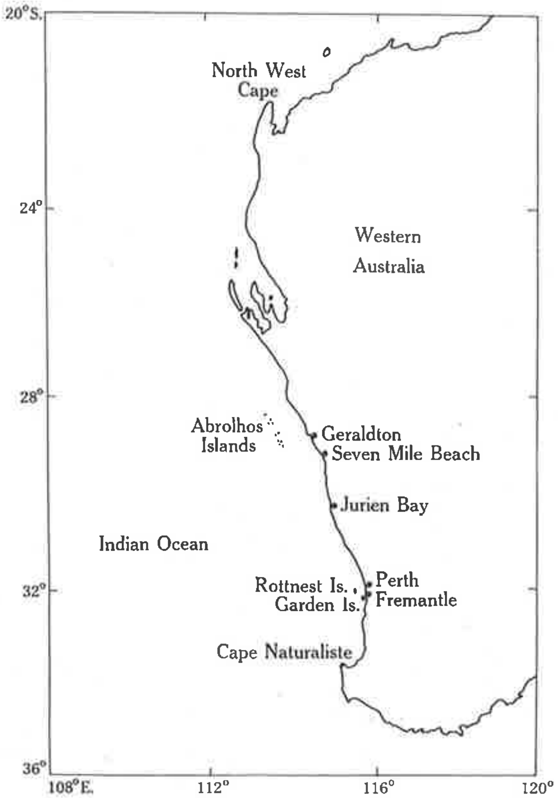

Fig. 1. Location of the sites referred to in the text.

The collectors were checked monthly after each new moon period (when most larvae settled). All settlement took place at the puerulus stage. The young rock lobsters were removed from collectors either as puerulus larvae or after they moulted into very small post-puerulus juveniles.

No quantitative value (in terms of absolute density) can yet be placed on the number of animals caught by the collectors. However, Phillips (1972) has shown that even single collectors were adequate to describe trends in settlement from month to month and from year to year so that the results of catches per collector at different sites are comparable.

Density of Juveniles

Density of combined age groups (ages 2–7 years) has been measured on shallow test reefs at Garden Island (since 1965), Jurien Bay (since 1971), and Seven Mile Beach (since 1970) using the single census trap–mark–recapture method described by Chittleborough (1970). Estimates of total population density for the beginning of each year are summarized in Table 1.

Table 1. Density (number per hectare) of juvenile rock lobsters in January each year as measured by trap–mark–recapture technique on test reefs

Locality	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
Garden Island										
Density	5144	2834	5386	1753	1343	1958	1811	1402	1877	1896
S.E.	119	152	223	94	61	111	107	62	134	179
Jurien Bay										
Density	—[A]	—	—	—	—	—	4824	1290	1635	4068
S.E.							458	109	168	410
Seven Mile Beach										
Density	—	—	—	—	—	11830	10130	9374	11863	19587
S.E.						798	646	721	650	882

[A] Not measured.

In order to follow the strength of individual year-classes, it is necessary to separate these measurements of total density into individual age groups. As shown by Chittleborough (1970, figs 3, 4) it is usually possible to separate those aged 2 years and 3 years by means of the polymodal size composition of the catches, but older groups are not often distinguishable. In Table 2 the population densities as measured from catches at Garden Island have been partially separated into age groups in this way.

Table 2 shows clearly that juvenile rock lobsters aged 2 years were poorly represented in the catches upon which the estimates of population density were made. This was due to dominance by larger juveniles in competition for food, as shown experimentally by Chittleborough (1974*a*). Amongst the group 2 years of age, only the more aggressive seekers of food have a high probability of capture and as these tend to be the same individuals in each trapping of a trap–mark–recapture experiment, the technique estimates only the more highly catchable fraction of the 2-year age group. As the degree of dominance may vary with the density of the older individuals and also with changes in the availability of food species, little reliance can be placed upon estimates of density of 2-year-old rock lobsters made in this way.

Table 2. Juvenile rock lobsters at Garden Island in January each year

Densities (number per hectare) as estimated from trap–mark–recapture technique, separated into age groups on basis of polymodal size composition

Age (years)	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
2	189	716	168	21	62	83	12	43	309	36
3	3245	1070	3324	317	265	875	537	92	971	1200
4–7	1710	1048	1894	1415	1016	1000	1262	1267	597	660

The baited-trap technique appears to have comprehensively sampled the juvenile rock lobsters aged 3 years so that these estimates of density are more reliable. If accurate estimates can be obtained of natural mortality operating upon juveniles each year, these could be applied to the densities of those aged 3 years in order to build up a picture of survival of individual year-classes through the years as juveniles.

Earlier estimates of juvenile natural mortality coefficients made by Chittleborough (1970), based on the rate of decline in total population density during that part of the year when migration was minimal, are suspect because of the poor representation of those aged 2+ years. At the beginning of the year, a few of this age group are so small that they can escape through the mesh of the traps. Later in the year they have grown sufficiently to be retained in the traps and also are better able to compete for access to the baited traps. Hence estimates of natural mortality coefficients would be better based upon changes in density of the population from 3 years of age and over.

Table 3. Juvenile rock lobsters on Garden Island test reefs

Densities (number per hectare) and mortality coefficients within each year for those aged ≥3 years

Year	Date	Initial density	Date	Density in spring	Time (t) (weeks)	M_t	M_{Yr}
1965	11 Jan.	4955	2 Sept.	2229	33	0·799	1·259
1966	20 Jan.	2118	17 Aug.	1804	30	0·161	0·278
1967	7 Jan.	5218	7 Sept.	1881	35	1·020	1·516
1968	25 Jan.	1732	19 Sept.	1170	34	0·392	0·600
1969	19 Jan.	1281	17 Aug.	1072	30	0·178	0·309
1970	7 Jan.	1875	2 Sept.	1598	34	0·160	0·244
1971	20 Jan.	1799	25 Aug.	1352	31	0·286	0·479
1972	13 Jan.	1359	15 Sept.	1018	35	0·289	0·429
1973	5 Jan.	1568	24 Aug.	960	33	0·491	0·773
1974	16 Jan.	1860	25 Aug.	1464	32	0·239	0·389

Table 3 shows the calculation of natural mortality coefficients for juvenile rock lobsters at Garden Island, based upon the same procedure as used by Chittleborough (1970), but deleting the poorly sampled 2+ years age group. Natural mortality coefficients were derived similarly for juveniles at Jurien Bay and at Seven Mile Beach.

In order to demonstrate how an index of the strength of a year-class through several successive years has been derived, the year-class of 1963–64 at Garden Island is used as an example:

The density of the 1963–64 year-class at 3 years of age (i.e. in January 1967) was 3324 per hectare (Table 2). During 1967 the natural mortality coefficient of those aged 3 years and over was 1·516 (Table 3). Therefore the density of this year-class surviving at 4 years of age (in January 1968) was

$$3324\exp(-1{\cdot}516) = 730 \text{ per hectare.}$$

During 1968 the natural mortality coefficient was 0·600 (Table 3) so that the density of this year-class surviving at 5 years of age (in January 1969) was

$$730\exp(-0{\cdot}600) = 401 \text{ per hectare.}$$

To back-calculate the density of this year-class for January 1966 (i.e. at 2 years of age), the mortality rate during 1966 should be divided into the density measured in

January 1967 (at 3 years of age). While the mortality coefficient for 1966 was based on data from the segment of the population aged 3 years and over, the coefficient itself was partly dependent upon those aged 2 years present in the reef population since the age groups present on a reef at a particular time interact and are acted upon by the same environmental pressures. If there was no additional mortality due to competition between age groups, the mortality rate of those aged 2 years would be the same as that of the older juveniles present at the same time. However, because those aged 2 years have been shown to compete less successfully for food (Chittleborough 1974*a*), their mortality is likely to be higher than that of the older juveniles. Thus the mortality calculated for those aged 3 years and over may be taken as a minimum estimate of the mortality of those aged 2 years present on the reef at the same time, being closer to the actual mortality of the younger age group when the density of the older juveniles is low. As the density of those aged 3 years in January 1967 was 3324 per hectare and the natural mortality coefficient during 1966 was 0·278 (Table 3), the minimum density of the 1963–64 year-class in January 1966 (at 2 years of age) was

$$3324/\exp(-0\cdot278) = 4400 \text{ per hectare.}$$

Table 4 shows the estimated densities of various year-classes at the three localities calculated as given in the above example. Owing to relatively low intensity of sampling at Jurien Bay the data for that locality are less reliable. This applies most particularly to the estimates of mortality coefficients so that at Jurien Bay more reliance should be placed on estimates for those aged 3 years than upon other age groups.

Table 4. Estimate of year-class strength (number per hectare) for juvenile western rock lobsters on test reefs

Locality	Age (years)	Year-class: Season of hatching									
		61–62	62–63	63–64	64–65	65–66	66–67	67–68	68–69	69–70	70–71
Garden Island	2	—[A]	3800	4400	1400	500	1200	700	150	1500	2600
	3	3245	1070	3324	317	265	875	537	92	971	1200
	4	921	810	730	174	195	685	333	60	448	813
	5	697	178	401	128	152	424	217	28	304	—
Jurien Bay	2	—	—	—	—	—	—	—	500	700	700
	3	—	—	—	—	—	—	1293	33	308	499
	4	—	—	—	—	—	—	80	15	232	139
	5	—	—	—	—	—	—	35	11	65	—
Seven Mile Beach	2	—	—	—	—	—	—	6200	6100	5100	12 100
	3	—	—	—	—	—	5779	3825	2318	2135	7591
	4	—	—	—	—	—	3540	1461	978	1339	3522
	5	—	—	—	—	—	1352	616	613	621	—

[A] Not measured.

Recruitment to the Fishery

A method for estimating density of potential emigrants based upon size composition of the population on the shallow reefs shortly before the emigration of each November has been set out by Chittleborough (1970).

An independent index of the relative abundance of new recruits within the fishery is the catch per unit effort achieved by fishermen operating at depths of 5–18 m from the opening of the fishing season (15 November) until they move their pots to deeper water during December. This period is locally known as the 'white' season, as most of the juveniles are newly moulted with very pale shells. These data were obtained from detailed logbooks maintained by fishermen.

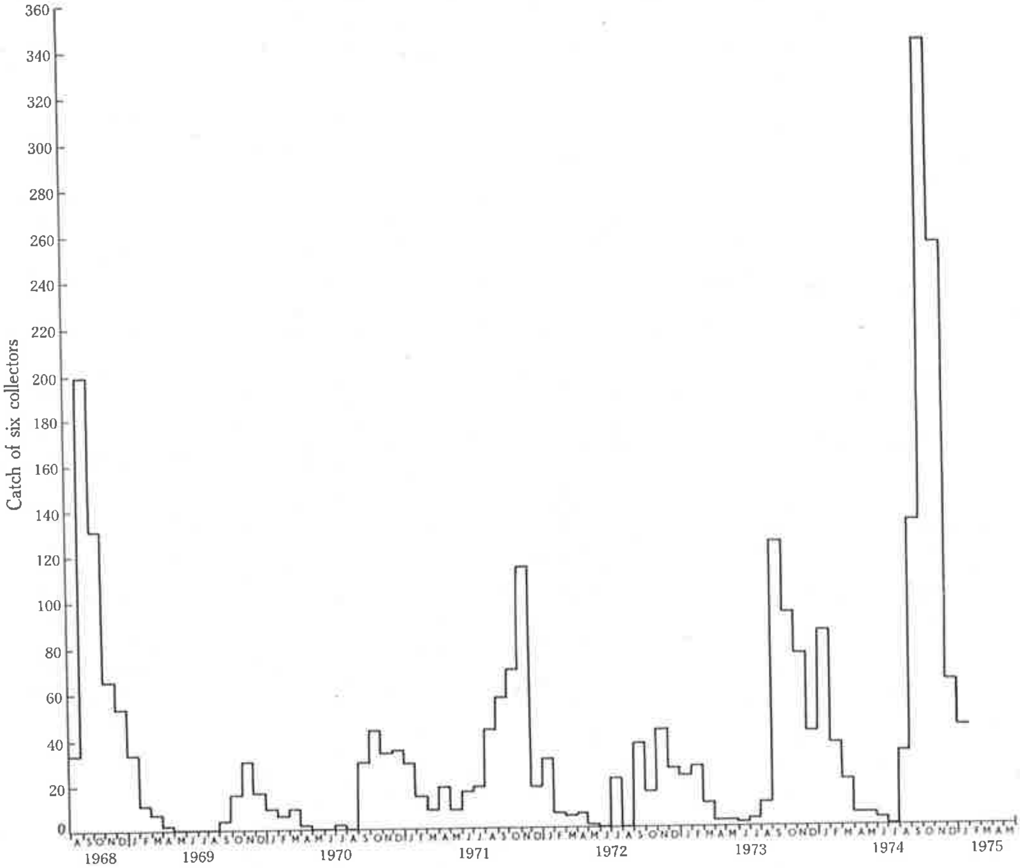

Fig. 2. Catches of six collectors at Seven Mile Beach.

Results

Larval Settlement

The seasonal pattern of settlement of puerulus larvae is illustrated in Fig. 2 where the monthly catches of six collectors maintained at Seven Mile Beach have been combined. In most seasons there has been a discrete period of settlement between July–August of one year and April–May of the subsequent year, with a marked peak between September and November. Little or no settlement occurred during winter so that settlement of successive year-classes could be separated quite easily.

Collectors at other localities showed similar seasonal trends in larval settlement, with some minor differences in the month of peak settlement.

The relative densities of settlement of the puerulus larvae (expressed as the mean number per collector per season) at Garden Island, Jurien Bay and Seven Mile Beach are compared in Fig. 3. This shows that settlement along the coast fluctuated very greatly in density from year to year, and also that settlement in the centre of the coastal range, i.e. Seven Mile Beach, varied around a higher mean level than that part of the coast which is nearer the periphery of the population, i.e. Garden Island (as suggested by Chittleborough 1970).

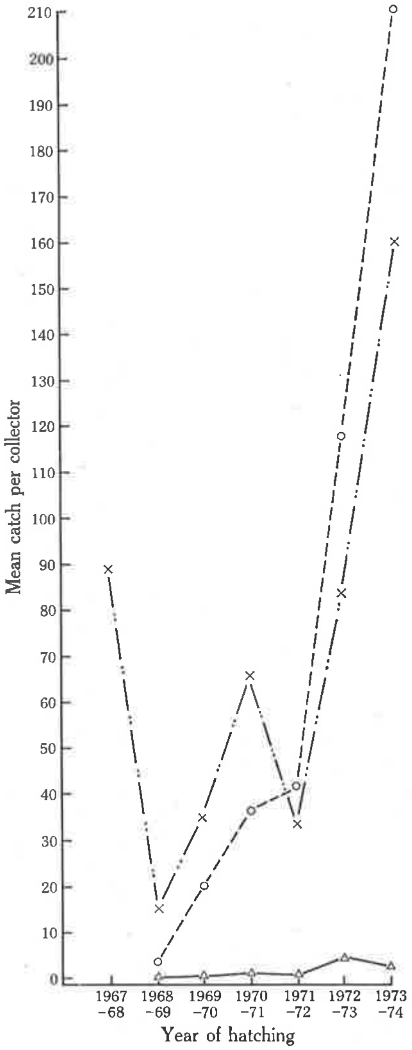

Fig. 3. Relative densities of settlement of the puerulus larvae at Garden Island (△), Jurien Bay (○) and Seven Mile Beach (×).

Low levels of settlement were recorded at all three sites in 1969–70 (the year-class of 1968–69), but again the level of settlement improved from the periphery to the centre of the population.

Since the poor settlement of the 1968–69 year-class, annual settlement at Seven Mile Beach and Jurien Bay has improved steadily apart from a slight lapse in the settlement of the 1971–72 year-class. The most recent season of settlement (1973–74 year-class) has been the most successful since the collectors were put into operation. Settlement at Garden Island has shown similar trends except the catch of the 1973–74 year-class which did not rise.

Juveniles

Tables 1 and 4 show that the densities of juveniles at the centre of the population (Seven Mile Beach) were much higher than towards the periphery (Garden Island), as was the case with larval settlement.

At Garden Island, where the longest series of measurements of density have been made, there have been large fluctuations in year-class strength (Table 4), juveniles aged 2 years being strongest from the year-classes of 1961–62 to 1963–64, relatively weak from the year-classes of 1965–66 to 1968–69, and showing some improvement in the most recent samplings. The poorest year-class at Garden Island has been that of the 1968–69 spawning; this year-class was also the poorest at Jurien Bay (as evidenced by the more reliable data for those aged 3 years). While the overall levels at Seven Mile Beach were better, the 1968–69 year-class was not particularly strong, nor was that of 1969–70, but the following year-class was much improved.

In general there has been good consistency in the indices of year-class strength obtained from larval collectors (at settlement) and those derived from measurements of density of juveniles aged 2 or 3 years. However, survival through to age 5 years (pre-recruits to the fishery) does not mirror the pattern of year-class strength at or soon after settlement. As shown by Chittleborough (1970), natural mortality of juveniles varies with the overall density of juveniles on that reef. Dominance of larger (older) juveniles (Chittleborough 1974*a*) may mean that survival within a particular year-class depends to a large extent upon the strength of the one or two preceding year-classes. Thus at Garden Island, survival of the 1962–63 year-class from age 2 years to age 5 years (a period of strong year-classes) was only 4·7%, whereas the corresponding survival of the 1966–67 year-class (preceded by weak year-classes) was 35·6%.

The fate of individual year-classes represented on the test reefs at Garden Island and Seven Mile Beach is illustrated in Fig. 4. It is clear that a year-class which was relatively strong initially is not necessarily particularly strong by the time it reaches 5 years of age. Despite much higher settlement of puerulus larvae at Seven Mile Beach (Fig. 3), the densities of those surviving at 5 years of age were little above those at Garden Island (Fig. 4).

Recruitment to the Fishery

The estimated density of those juveniles surviving on the shallow reefs at 5 years of age (Table 4) might be considered as an indication of the potential level of recruitment to the fishery. In the vicinity of Garden Island, the very poor year-class of 1968–69 appeared to be linked with the relatively low mean catch per unit effort for the shallow (5–18 m) water 'white' fishing of 16 November to 31 December 1973. However, the regression of mean catch per unit effort of the local 'white' fishery, on the density of those aged 5 years on the 'nursery' reefs in the same year, gave a correlation coefficient of 0·503 which was not significant and an intercept of 1·716 indicating that a not inconsiderable catch would be achieved even if one group aged 5 years was lost altogether. One reason for this is that emigration from the 'nursery' reefs is determined largely by size so that some emigrants are 6 or 7 years of age while others may be faster growing individuals aged 4 years.

For this reason, the method described by Chittleborough (1970) based upon size composition of the population on the shallow reefs shortly before the emigration of each November, may give a more reliable estimate of the potential recruitment to

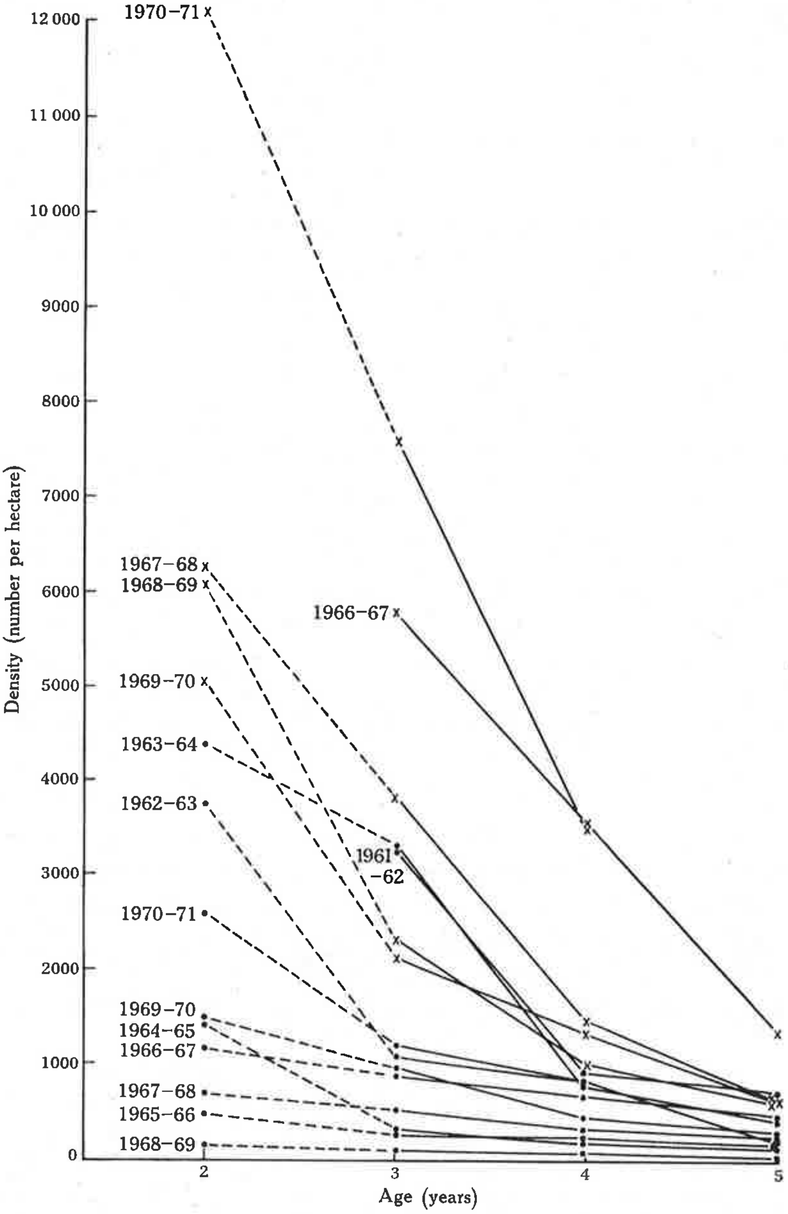

Fig. 4. The change in density of individual year-classes on the test reefs at Garden Island (●) and Seven Mile Beach (×).

the fishery. Table 5 shows estimates made in this way of potential recruitment levels each year at Garden Island, together with the mean catch per pot-lift achieved by fishermen operating nearby in depths of 5–18 m from the opening of the fishing season (15 November) until they moved their pots to deeper water during December.

The regression of mean catch per unit effort (W) from the 'white' fishery on the estimated density of potential recruits (R) from the shallow reefs gave the relation

$$W = 0\cdot866+0\cdot00183R,$$

with a correlation coefficient (r) of 0·676 which is significant at the 5% level.

Thus there is a positive relationship between the density of the larger juveniles on the shallow coastal reefs during the latter part of a year and the success of the commercial fishery in adjacent waters at the opening of the next fishing season (November–December). Part of the reason why the correlation coefficient was not even higher may be because of fluctuations from year to year in catchability coefficient (Chittleborough 1970), making the commercial catch per unit effort a less precise measure of abundance of rock lobsters on the fishing grounds. The value of the intercept of the above regression indicates that between one-third and one-half of the commercial catch at that time may not have been recruited that season from the adjacent coastal reefs.

Table 5. Estimated potential recruits on Garden Island test sites each spring and mean catch rates in adjacent fishery at opening of fishing season (16 November to 31 December)

	1965	1966	1967	1968	1969	1970	1971	1972	1973
Potential recruits (number per hectare)	504	756	400	586	502	558	574	671	338
Mean catch /effort in adjacent fishery (5–18 m)	1·37	1·96	1·70	2·26	1·61	1·85	2·09	2·38	1·50

Discussion

The various components of the environment likely to affect recruitment in this population have been examined by Chittleborough (1975) who concluded that the predominant factor limiting survival and growth of juveniles is the limited availability of food on the coastal reefs. The level of recruitment from a particular year-class depends on (i) its initial density, i.e. at the time of larval settlement; (ii) the strength of other year-classes pre-existing on the 'nursery' reefs; (iii) variations in density of food species; and (iv) variations in density of predator species.

The holding capacity of 'nursery' reefs through to the recruit stage (5–7 years of age) does not appear to differ greatly from point to point along the coast so that density-dependent mortality of juveniles results in similar numbers surviving to recruitment irrespective of wide differences in density at or soon after larval settlement (Fig. 4), provided that the initial stocking rate is sufficiently high. At Garden Island several poor year-classes have resulted in the reefs carrying less than their holding capacity (Fig. 4), culminating in the particularly weak year-class of 1968–69 which resulted in a low level of recruitment to the nearby fishery in 1973. Reasonable recruitment can occur from year-classes which initially were not particularly strong, provided that competition from older juveniles is low, food supply adequate, and predation by other species low.

The results presented here show that a prediction of the relative success of the 'white' fishery (at the opening of each fishing season) can only be made following the appearance of particularly poor year-classes. As mentioned by Hancock (1971), following the low settlement of puerulus larvae on the collectors in 1969–70 and low density of early juveniles, it was predicted in 1971 that low catch levels would be likely in 1972–73 and even lower levels likely at the opening of the 1973–74 season. This prediction was borne out by the catches of these two years (Anon. 1974), the 'white' season of 1973–74 being the poorest on record, particularly in the Fremantle area (reflecting trends in the Garden Island research area).

The appearance of a very strong larval settlement such as that of 1974–75 at Seven Mile Beach (Fig. 3), does not necessarily mean that a high level of recruitment to the fishery can be predicted for 1978–79. In that instance the preceding year-classes are relatively strong so that the year-class of 1973–74 faces intense competition and high mortality while on the 'nursery' reefs.

The very high (and density-dependent) wastage amongst young juveniles following particularly heavy settlement of larvae on reefs already well stocked with older age groups raises the possibility for cropping off part of the excess for other purposes, without affecting the level of subsequent recruitment to the fishery. This cropping might be applicable to those aged 1 or 2 years; juveniles from 4 to 5 years of age would still require full protection as the immediate pre-recruits have already been exposed to the density-dependent natural mortality. The excess young (1 or 2 years of age) might be used to stock underpopulated reefs, or reared in captivity under optimal conditions. Both prospects have been tested experimentally with some success (Chittleborough 1974*b*, 1974*c*, and unpublished data), but it has yet to be demonstrated that either would be economical.

Towards the centre of the coastal distribution of this population, the wide fluctuations in year-class strength and the extremely high level of the year-class most recently measured (Fig. 3), indicate that the high exploitation rate which has been maintained for some years in the fishery (Bowen and Chittleborough 1966) has not reduced the breeding stock to the point where recruitment is endangered.

Acknowledgment

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Growth of Juvenile *Panulirus longipes cygnus* George on Coastal Reefs Compared with Those Reared Under Optimal Environmental Conditions

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Abstract

The growth of a group of six juvenile western rock lobsters raised for 6 years in aquaria was well represented by the von Bertalanffy equation

$$l_t = 113\cdot47[1-\exp\{-0\cdot459(t-1\cdot045)\}].$$

Using single-moult increments as well as annual growth (determined by shift in modal length and returns of tail-punched and tagged individuals) growth of juveniles in the wild population was compared with that of those reared under near-optimal conditions. At three of the four localities studied, growth was retarded. Growth was most suppressed at the locality where the density of juveniles was highest. However, at a locality where nursery reefs carried relatively low densities in recent years, growth was still well below that achieved in aquaria.

Limited food resources on shallow nursery reefs was suggested as the main reason for the retardation of growth. Where the shortage was less severe, competition amongst juveniles resulted in the growth of younger age-groups (2+ and 3+ years) being more retarded than older juveniles, and that of females being more retarded than that of males. Upon emigrating to deeper waters (mainly at 5 and 6 years of age), juveniles showed a marked acceleration in growth rate. As juveniles have distinct growth phases with different environmental pressures applying at each, growth in the wild population at most localities is not well represented by a single von Bertalanffy equation.

Introduction

After a planktonic phase of 9–11 months, larvae of the western rock lobster return to settle along the western coast of Australia. Juveniles then spend 4 or 5 years gathered on shallow nursery reefs before moving offshore and being recruited to the fishable stock and later to the breeding population.

Initial studies of recruitment were concerned with numbers and survival. Chittleborough (1970) and Chittleborough and Phillips (1975) found that at times the settlement of puerulus larvae on shallow coastal reefs exceeded the holding capacity of those reefs so that density-dependent mortality amongst the juveniles limited the level of recruitment to the fishery.

From experiments in aquaria under controlled environmental conditions, Chittleborough (1975) concluded that availability of food was likely to be the major limiting factor amongst juveniles on the coastal reefs. Dall (1975) developed a field technique for assessing the nutritional state of western rock lobsters and showed that some juveniles on these reefs were in a poor state of nutrition.

Chittleborough (1974*a*) reared a group of western rock lobsters from the puerulus larval stage to maturity (at 4·9–5·7 years of age) in aquaria. The growth of these individuals, raised under near-optimal conditions, is used here as a yardstick against which are compared the growth of juveniles on shallow reefs at several points along the coast of Western Australia.

The choice of a scientific name for the western rock lobster has been under debate. Previously regarded as a population of *Panulirus longipes* (Milne Edwards), it was described as a new species *P. cygnus* by George (1962). Subsequently, Chittleborough and Thomas (1969) advanced reasons why it should be given subspecific status. However, the use of the term 'form' instead of 'subspecies' in that paper contravened Article 45 of the code of nomenclature adopted by the International Commission on Zoological Nomenclature (1964). Accordingly the original name of *P. longipes* has been used in subsequent papers.

Although for management purposes these western rock lobsters may be regarded as a unit stock, the oceanic larvae from this population are not completely separated from the phyllosoma larvae of tropical populations of *P. longipes* in the Indian Ocean (Chittleborough and Thomas 1969, Fig. 2). In recent years near-adult specimens having pale spots on the legs (characteristic of specimens of *P. longipes* from the type locality of Zanzibar) have been taken occasionally from reefs on the coast of Western Australia. Apparently there is some gene flow from the north. While this in itself does not preclude the local population from specific rank, on the evidence available it is proposed that this population on the western coast of Australia be given subspecific rank *Panulirus longipes cygnus* George.

Modern methods for genetic analysis of populations, whether morphometric (Phillips *et al.* 1973) or molecular (Nei 1975), may be needed to resolve the taxonomic status of the western rock lobster. Perhaps the best approach, initially at least, would be to hold adults from different populations together in aquaria, and determine the occurrence and viability of cross matings. This should enable a decision to be made whether each population is sufficiently isolated genetically to warrant specific rank.

Methods

Six western rock lobsters reared in captivity from the puerulus larval stage for 6 years were held in an open-circuit seawater system and fed excess food daily (mussels, abalone, or fish). The temperature of the incoming seawater was held at 25°C throughout most of the period. These animals were held together as a group, since it was shown by Chittleborough (1975) that the growth rate is depressed for animals held in isolation. Individuals were identified by distinctive punching of holes (3 mm diameter) in the telson or uropods. Although these holes healed over after several moults, the code could still be read from the scar tissue. For rapid checking of individuals without handling, a number was painted on the carapace of each individual using an epoxy-resin paint (Chittleborough 1974*b*). The date of each moult was recorded and a few days later when the shell had hardened the carapace was measured and the number re-painted on the new shell.

Other groups of juveniles maintained in aquaria for 12 months in experiments on growth and survival under selected environmental conditions (Chittleborough 1975) afforded further comparative data.

The size of a western rock lobster was recorded as the carapace length measured (to 0·1 mm) along the mid-dorsal line from the ridge behind the eyes (between the rostral horns) to the posterior margin of the carapace. Body weight of live animals was measured after removing free water as described by Chittleborough (1975).

Growth of juveniles in the wild population was measured on shallow coastal reefs (0–5 m depth) at Garden Island (32°10′S.), Jurien Bay (30°19′S.), Cliff Head (29°31′S.), and Seven Mile Beach (29°08′S.). Regular trapping yielded samples of sufficient size to enable the progression of modal size groups to be followed (Chittleborough 1970). The younger age-groups could be distinguished in these polymodal samples. At Garden Island (where more data have been obtained), the ranges in carapace length shown in the following tabulation were selected as approximate limits for these age-groups at the beginning of a year (January):

	Carapace length (mm) at 2 years	 3 years	 4 years
Males	29–40	41–53	54–68
Females	28–39	40–51	52–66

These ranges also applied reasonably well to polymodal distribution of sizes recorded at Seven Mile Beach and Jurien Bay, although in the samples from these localities the modal size group for those 4 years of age was often difficult to distinguish. The size ranges at ages given above were not applicable at Cliff Head.

The use of the western rock lobster tag and the method of tail punching were as described by Chittleborough (1974*b*). When this tag was being developed, tests showed that it did not affect the growth rate significantly. In most cases tail punching and tagging were carried out during January each year so that recaptures during autumn (1–3 months after marking) could be used to measure a single moult increment. Because juveniles remain on the 'nursery' reefs for several successive years and have a very limited home range on a reef (Chittleborough 1974*c*), repeated recaptures of a tagged individual are possible over a long period and thus a number of measurements of growth rate may be made on one individual. The longest-term recapture of a tagged western rock lobster was 5 years after tagging.

Table 1. Single-moult increments in carapace length (mm) of six juvenile western rock lobsters reared under near-optimal conditions in aquaria for 6 years

Age (years)	Males No.	 Mean	 s.e.		Females No.	 Mean	 s.e.	Total No.	 Range	 Mean	 s.e.
2+	15	5·0	0·2	n.s.	14	5·6	0·2	29	3·6–7·6	5·3	0·2
										n.s.	
3+	11	5·1	0·5	n.s.	12	4·3	0·4	23	1·1–7·3	4·7	0·3
										*	
4+	11	3·5	0·5	n.s.	10	4·0	0·3	21	1·8–5·6	3·8	0·2
										***	
5+	5	2·5	0·4	n.s.	8	2·0	0·3	13	1·1–3·8	2·2	0·3
										***	
6+	5	1·4	0·3	n.s.	9	0·8	0·1	14	0·0–2·2	1·0	0·2

* $0\cdot01 < P < 0\cdot05$. ** $0\cdot001 < P < 0\cdot01$. *** $P < 0\cdot001$. n.s., Not significant.

Size Increment per Moult

Moulting in Aquaria

B. F. Phillips, N. A. Campbell and W. A. Rea (unpublished data) showed that the size increment per moult of very early juveniles increased during the first postlarval year, reaching an asymptote at about 2 years of age. Table 1 shows that in the group reared in the aquarium for 6 years under near-optimal conditions, the peak in moult increment was maintained during the third year of life (age 2+ years), changed little in the following year (age 3+ years), but declined thereafter. Within this group raised under conditions of minimal environmental stress there was no significant difference in moult increment between the sexes.

Moulting in Natural Populations

Single-moult increments in carapace length recorded from tagged and tail-punched juveniles at various test sites along the coast (Table 2) showed some marked differences in comparison with those recorded in aquaria (Table 1).

Table 2. Single-moult increments in carapace length (mm) of juvenile western rock lobsters in reef populations for 1970–74

Age (years)	Males				Females		
	No.	Mean	s.e.		No.	Mean	s.e.
Garden Island							
3+	80	4·3	0·1	*	87	4·0	0·1
		*				n.s.	
4+	80	4·7	0·1	**	128	4·1	0·1
		n.s.				n.s.	
5+	10	5·4	0·3	***	20	3·8	0·1
Jurien Bay							
4+	16	4·6	0·4	n.s.	13	4·0	0·5
						n.s.	
5+					8	5·0	0·5
Seven Mile Beach							
3+	76	3·0	0·1	n.s.	97	3·0	0·1
		n.s.				n.s.	
4+	38	3·1	0·2	n.s.	83	2·9	0·1
		n.s.					
5+	10	3·0	0·4				

* $0 \cdot 01 < P < 0 \cdot 05$. ** $0 \cdot 001 < P < 0 \cdot 01$. *** $P < 0 \cdot 001$.
n.s., Not significant.

At Garden Island the mean increment per moult for males and females aged 3+ years was significantly ($P = 0 \cdot 001$) less than that of those of the same age held under near-optimal conditions in aquaria. Moult increments of males increased from ages 3+ to 5+ years, whilst those of females did not vary significantly between these age groups. In each of the three groups the moult increment of females was significantly below that of males (Table 2).

At Jurien Bay the rather sparse data on single-moult increments were similar to those from Garden Island.

At Seven Mile Beach single-moult increments were not only less than those recorded at Garden Island but also there were no significant differences between sexes or between age groups (Table 2).

Where there were sufficient numbers of observations a check was made for possible variations from year to year in single-moult increments. At Garden Island there were some significant differences (Table 3), more evident in the females than in the males. Single-moult increments were reduced in 1971 and to a lesser extent in 1967 (females). The annual fluctuations in moult increments showed no relation to variations in density of juveniles on reefs at Garden Island.

Table 3. Single-moult increments in carapace length (mm) of juvenile western rock lobsters on reefs at Garden Island in specified years

Year	Females						Males					
	Age 3+ years			Age 4+ years			Age 3+ years			Age 4+ years		
	No.	Mean	s.e.	No.	Mean	s.e.	No.	Mean	s.e.	No.	Mean	s.e.
1965	59	4·4	0·1	71	4·6	0·1	100	4·7	0·1	60	5·0	0·2
		**						n.s.			n.s.	
1967	64	3·8	0·1		n.s.		41	4·4	0·2	9	5·2	0·3
		**						n.s.			n.s.	
1968	15	4·6	0·3	41	5·0	0·1	10	4·7	0·3	35	5·4	0·1
		n.s.			n.s.			n.s.				
1970	12	4·4	0·2	16	4·9	0·3	17	4·9	0·2		***	
		n.s.			n.s.			n.s.				
1971	19	3·8	0·2	51	3·6	0·2	12	4·3	0·2	37	4·2	0·2
					***						**	
1972		n.s.		33	4·6	0·2		n.s.		14	5·1	0·2
					n.s.						n.s.	
1974	45	4·0	0·1	24	4·0	0·3	43	4·2	0·2	16	5·3	0·3

* $0·01 < P < 0·05$. ** $0·001 < P < 0·01$. *** $P < 0·001$. n.s., Not significant.

Growth Rates

Growth Rate in Aquaria

The group of six western rock lobsters brought into the aquarium as puerulus stage larvae of the same year-class and reared for 6 years under near-optimal conditions affords a useful set of data from which to derive a growth curve against which growth rates measured in the field can be compared.

By plotting the increase in carapace length during each year against the carapace length of the same indiviual at the beginning of the year (Fig. 1), an estimate can be made of L_∞ (from the intercept on the horizontal axis) and of K (from the slope of the regression). This is similar to the method of Manzer and Taylor (1947) in which individual data are plotted rather than the Ford–Walford plot in which the mean size at each age is used. As Hancock (1965) pointed out, the former method is suitable provided that sufficient age-groups are represented. Either approach could have been used for the aquarium-reared western rock lobsters since precise ages were known, but the Manzer–Taylor plot was used since individual ages were not known so precisely in the case of the field data.

Within the aquarium-reared group (Fig. 1) there was no significant difference either in slope or in intercept between males and females so the data could be represented by a single regression. The correlation coefficient of the regression shown in Fig. 1 was $r = 0·932$. The resulting von Bertalanffy growth equation, derived as described by Gulland (1969), had the form:

$$l_t = 113·47[1-\mathrm{e}\{-0·495(t-1·045)\}].$$

This growth curve has been based mainly upon the juvenile phase since breeding commenced within this group when the females were 5–5·7 years of age and had a carapace length of 97–106 mm (Chittleborough 1974*a*). Inspection of Fig. 1 might suggest that the growth rate declined more rapidly after sexual maturity was reached, but by that time most of these individuals were already close to the asymptotic length. Deletion of the data after maturity did not reduce the slope of the regression significantly.

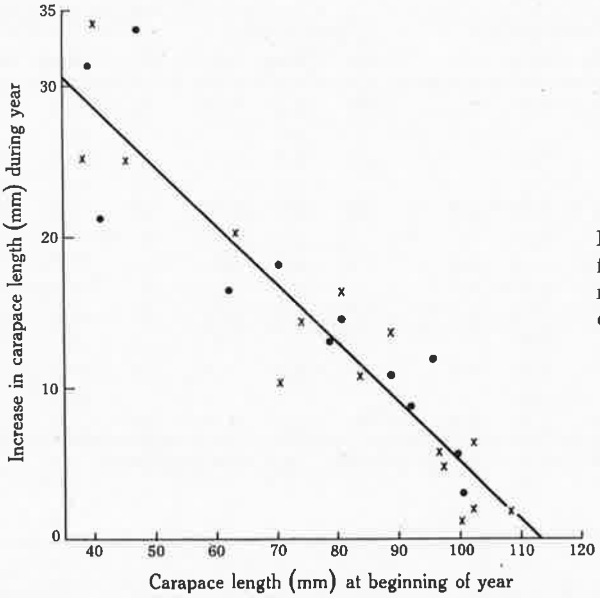

Fig. 1. Growth of male (●) and female (×) western rock lobsters reared in aquaria under near-optimal conditions.

The length–weight relation was not obtained from the group of western rock lobsters described above, because it was decided that these animals should be disturbed as little as possible. In other aquarium experiments carried out under controlled environmental conditions, juvenile western rock lobsters were measured and weighed after each moult as described by Chittleborough (1975). From these the regression of log body weight (W, in grams) on log carapace length (L, in millimetres) (Fig. 2) was

$$\log_{10} W = 2\cdot 8713 \log_{10} L - 2\cdot 8122 .$$

From this, the asymptotic weight (W_∞) corresponding to the L_∞ of 113·47 mm was 1·225 kg.

Growth Rates in Natural Populations

(i) *Shift in modal lengths*

Where a strong year-class can be recognized in samples taken at a particular locality (e.g. Chittleborough 1970, Figs 3 and 4) the progression of that clearly defined modal size group can be used to measure growth rate. Unfortunately modes are not always well defined. Juveniles aged 2+ years are clearly separated but older groups become progressively harder to distinguish. Mathematical approaches to the separation of age groups, such as that of Bhattacharya (1967), were attempted but often gave conflicting results except when modes were already obvious.

As a first approximation, modal lengths of males and females of 2, 3 and 4 years of age were identified by eye from the size composition of catches taken in nursery areas in January of each year. As the size intervals of measurements were small (1 mm), a sliding average of three size groups was applied to smooth the distribution as an aid in selecting modal lengths. The difference in modal length of those aged 2 years in January of one year and those aged 3 years in the following January gave a measure of the annual growth of the 2+ years age-group.

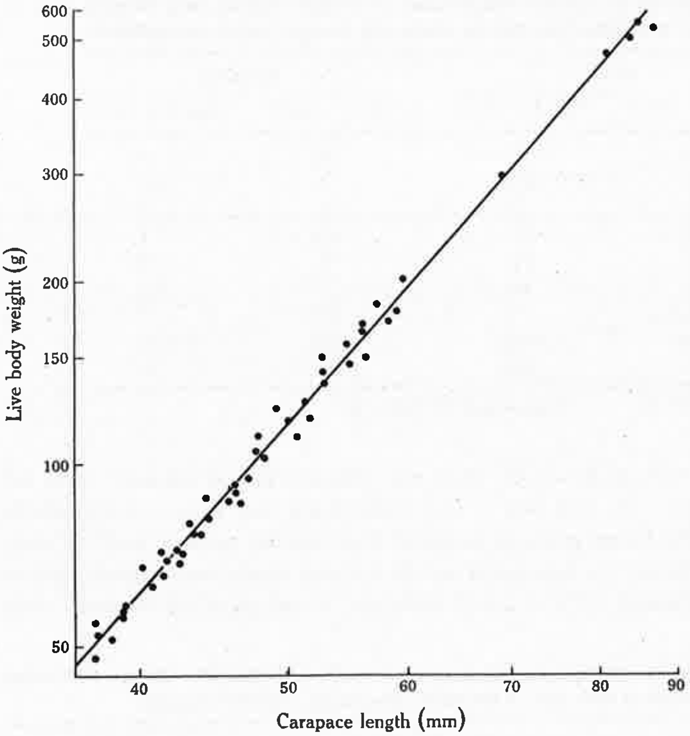

Fig. 2. Length–weight relation (logarithmic) for juvenile western rock lobsters in aquarium conditions.

The results of this approach applied to the data from the research reefs at Garden Island are summarized in Tables 4 and 5. The relatively strong year-class of 1963–64, which was preceded by another abundant year-class, had a lower growth rate (especially in the age-group 2+ years) than the relatively small year-class of 1969–70 which was preceded by an even smaller year-class (Chittleborough and Phillips 1975). Quite apart from some fluctuations in growth rate from one year to another, mean growth rate of juveniles on reefs at Garden Island was considerably less than for juveniles of the same ages held in aquaria (Table 5), even when groups exposed to the same ambient sea temperatures are compared. Growth rates of those aged 2+ years in the wild stock were relatively more depressed than those aged 3+ years, and growth of females was less than that of males.

At Seven Mile Beach the identification of modal sizes within samples of the population of juveniles was even more difficult but from those which could be separated (Table 6), annual growth tended to be lower than at Garden Island.

(ii) *Marking by coded tail punch or tag*

Tail punching was used in growth studies prior to the development of a suitable tag and also as a means of checking whether the tag interfered with growth (Chittleborough 1974*b*). Disadvantages of tail punching are that individuals cannot be identified and that the mark is seldom noticed by fishermen. Because of the latter problem research staff accompanied fishermen and examined catches taken immediately outside the nursery reefs at Garden Island.

Table 4. Annual growth in carapace length (mm) of juvenile western rock lobsters in Garden Island test area based on shift in modal size groups (where recognizable)

Year	Males		Females	
	Age 2+ years	Age 3+ years	Age 2+ years	Age 3+ years
1966	9½	12	9½	8
1967	?	11½	?	11
1968	13	?	?	?
1969	13½	11	12½	?
1970	14	13	13	9½
1971	?	10	?	11
1972	16	?	15½	?
1973	12½	13½	12½	10
1974	?	10½	12	8

+ Year-class of 1963–64. o Year-class of 1969–70.

Fig. 3 shows the growth of juveniles from the Garden Island nursery reefs tail punched in January 1966. By October a few individuals had grown considerably more than the others. The faster-growing juveniles had left the nursery reefs by early December, some being taken by fishermen up to 1·5 km from the marking site in depths of 7–15 m. Although only a small number of tail-punched western rock lobsters were recovered from the adjacent fishery, it may be significant that the seven faster-growing individuals were recaptured as dark-shelled 'red' rock lobsters while the slower-growing emigrant from the nursery reefs was taken as a pale 'white' phase (upon which the inshore fishery of late November and December is based). Fig. 3 shows that of those remaining on the nursery reefs 1 year after marking, annual growth showed little relation to the initial size at the time of marking.

Table 5. Mean annual growth in carapace length (mm) of juvenile western rock lobsters on Garden Island reefs compared with that of the same age-groups reared in aquaria

	Males		Females	
	2+ years	3+ years	2+ years	3+ years
Aquarium reared:				
optimum temp., excess food	28·4	17·4	28·4	17·4
Aquarium reared:				
ambient temp.,[A] excess food	20·4	14·9	20·4	14·9
Garden I., mean 1966–74	13·1	11·6	12·5	9·6
Garden I./Aquarium (ambient temp.)	64·2%	77·9%	61·3%	64·4%

[A] Ranging from 14·9°C in winter to 25·9°C in summer.

Tail punching in January 1967 gave slightly different results (Fig. 4) from those of the previous year. Overall, juveniles appeared to grow a little better than in 1966 (examined in detail below) but there were few very fast-growing individuals moving out to the adjacent fishery by December. Most of the larger animals (carapace length ⩾ 60 mm) marked in January 1967 had left the nursery reefs by December, the majority of these emigrating as the 'white' phase. Marking in subsequent years has given similar results to those of 1967 in that almost all of the emigrants to the fishery have been slow-growing older juveniles.

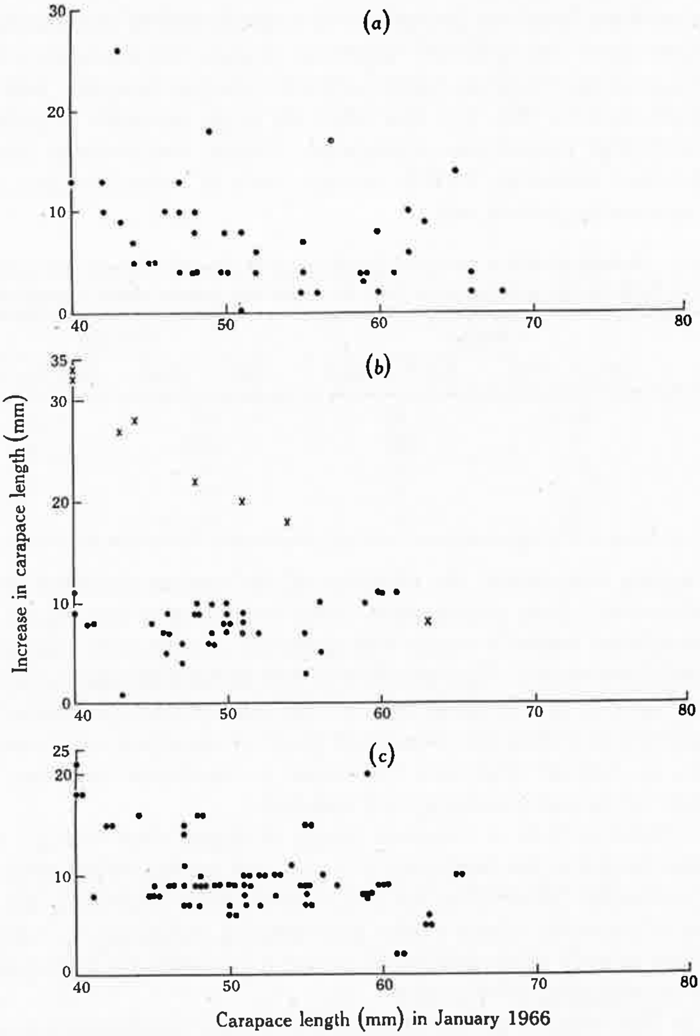

Fig. 3. Growth of juvenile western rock lobsters marked by coded tail punch in January 1966, on Garden Island nursery reefs. (*a*) January–October 1966. (*b*) January–December 1966. (*c*) January 1966–January 1967. ● Nursery reefs. × Adjacent fishery.

Tagging has the advantage over tail punching in that the tagged individual can be identified each time it is recaptured. Because of the restricted home range of juveniles on nursery reefs (Chittleborough 1974*c*) it has been possible to recapture a tagged individual up to 15 times over 2 or 3 years and so build up a more detailed picture of its growth while it is resident in a nursery reef (or until it moves out and is taken in the commercial catch).

Examples of data from tag recaptures at Garden Island are shown in Fig. 5. In some of these there were sufficient recaptures to show the seasonal cycle in growth rate with little or no growth from April to October during the cooler half of the year. Another feature shown in Fig. 5 is that when the larger juveniles migrated out from the nursery reefs their growth rate accelerated. Tagged western rock lobsters recaptured by fishermen operating outside nursery reefs at other localities consistently showed this increase in growth rate.

Table 6. Annual growth in carapace length (mm) of juvenile western rock lobsters in Seven Mile Beach area based on shift in modal size groups (where recognizable)

Year	Males		Females	
	Age 2+ years	Age 3+ years	Age 2+ years	Age 3+ years
1970	11	6½	12	5
1971	?	11½	11½	6½
1972	11½	?	?	7
1973	13½	?	14	?
1974	13½	?	12	?

In each tagging experiment the majority of the returns occurred within a few months of release and these results were biased according to the season of tagging. Short-term recaptures before a moult had occurred were heavily biased, having an apparent growth rate of zero. Recaptures after one moult still failed to give a realistic estimate of the growth rate as these reflected the single-moult increment component of growth without including the important facet of moulting frequency. For the above reasons, an interval of at least 10 months is considered necessary to afford a reliable measure of annual growth in rock lobsters.

When the annual growth of carapace length of tagged rock lobsters was plotted against carapace length at the beginning of a year, the growth of juveniles resident on nursery reefs at Garden Island (Fig. 6*a*) and at Seven Mile Beach (Fig. 6*b*) was clearly less than that of juveniles reared under near-optimal conditions in aquaria. Also at both localities growth of an individual during a year showed little relation to the initial size at the beginning of that year.

However, at Cliff Head (Fig. 6*c*) the growth of tagged individuals was comparable with that of individuals in aquaria. Some of those shown in Fig. 6*c* were residents of Cliff Head nursery reefs while others were juveniles transplanted from Seven Mile Beach to Cliff Head as described by Chittleborough (1974*c*). The 23 recaptures from Cliff Head had a mean carapace length of 57·6 mm when tagged. From the regression derived for the aquarium group, an animal of this length would be expected to have an annual growth of 21·8 mm. The mean annual growth actually recorded for these individuals at Cliff Head was in fact 21·8 mm.

Table 7 summarizes the annual growth of tail-punched and tagged western rock lobsters resident on nursery reefs at three localities, using the size ranges set out earlier in this paper to distinguish age groups. Whilst there were wide variations in individual growth rates, there were significant differences between localities. Growth rates were least at Seven Mile Beach, there being no significant differences between growth of males and of females or between those aged 3 years and those aged 4 years at this locality. Growth was slightly but significantly better at Garden Island.

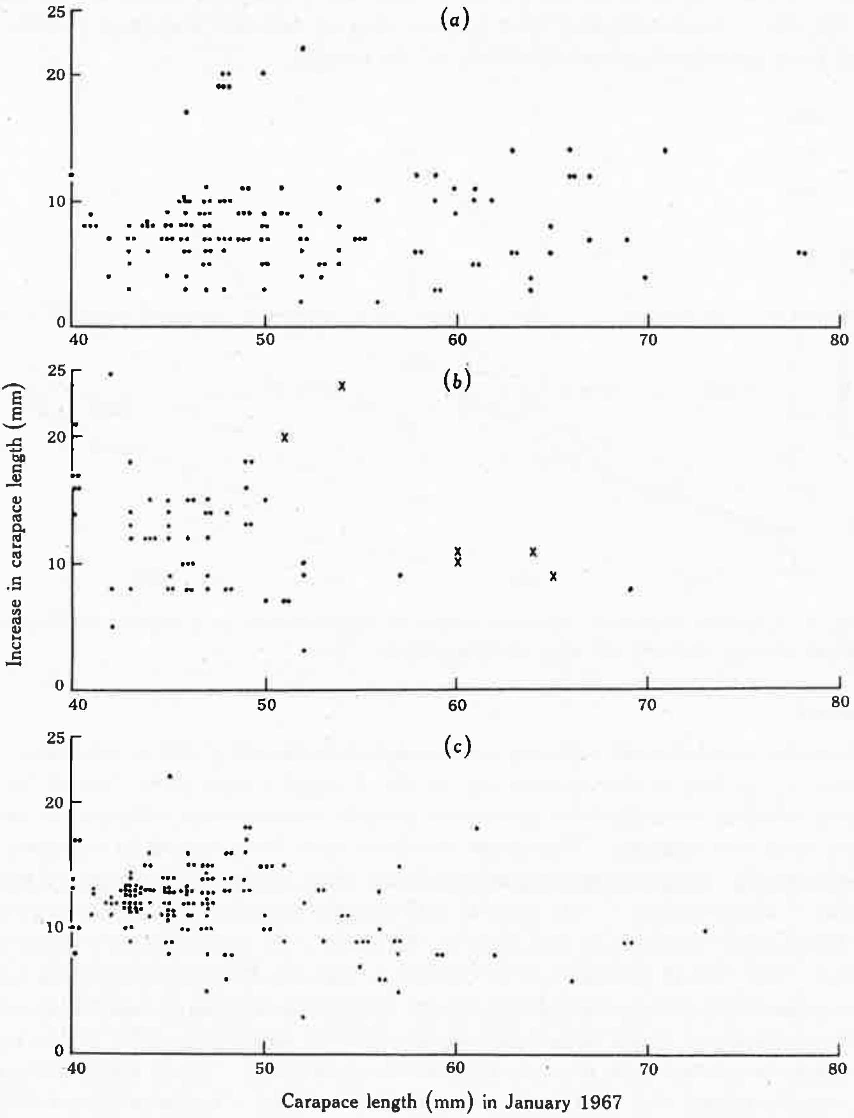

Fig. 4. Growth of juvenile western rock lobsters marked by coded tail punch in January 1967, on Garden Island nursery reefs. (*a*) January–October 1967. (*b*) January–December 1967. (*c*) January 1967–January 1968. ● Nursery reefs. × Adjacent fishery.

Here again there was no difference in growth rate between the sexes (within the same age-group) but there were significant differences between those aged 3 years and 4 years. At Jurien Bay the limited data indicated slightly better growth of males (aged 4 years) than in the previous areas and a significant difference in growth rate between the sexes. At Cliff Head age groups could not be distinguished but Fig. 6*c* shows that annual growth was similar to growth achieved under near-optimal conditions in aquaria.

Where there were sufficient data to measure the shift in modal lengths over a period of 1 year, the growth rates for those aged 3+ years determined by that method were similar to those obtained directly from tagging and tail punching (Tables 4–7), giving some confidence in the reliability of the results.

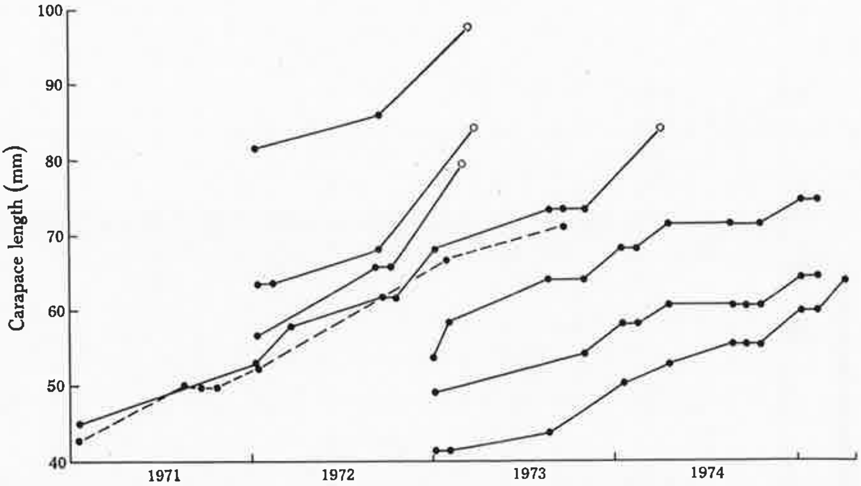

Fig. 5. Examples of growth (carapace length) of tagged western rock lobsters on Garden Island nursery reefs (●) and after moving offshore (○).

Discussion

Using the rapid growth achieved by an aquarium-reared group as an index of the potential for growth in this species, the results presented here show that at three of the four localities examined the growth of juvenile western rock lobsters on shallow nursery reefs was retarded. The extent of this is more than would be expected from the sub-optimal temperatures experienced on these reefs each winter (Table 5). Population density plays a role, growth rate being most severely depressed at Seven Mile Beach where the density was highest. However, this is not the only other factor involved. The overall growth rate at Garden Island has been relatively poor despite the low population density recorded in recent years (Chittleborough and Phillips 1975).

Measurements of single-moult increments afford a guide to another of the factors depressing the growth rate of rock lobsters in some areas. From aquarium experiments on the impact of a variety of environmental stresses it has been shown (Chittleborough 1975) that the primary effect of most of these factors upon growth was to reduce the frequency of moulting rather than to vary the size increment per moult. Only two types of stress were shown to inflict a very significant reduction of the size increment at moulting of intact western rock lobsters. These were a relatively severe shortage of food and a sub-lethal deficiency of oxygen during ecdysis. Measurements of dissolved oxygen in waters on these reefs have so far found oxygen to be in plentiful supply. In these shallow and usually turbulent waters over beds of sea-grasses and

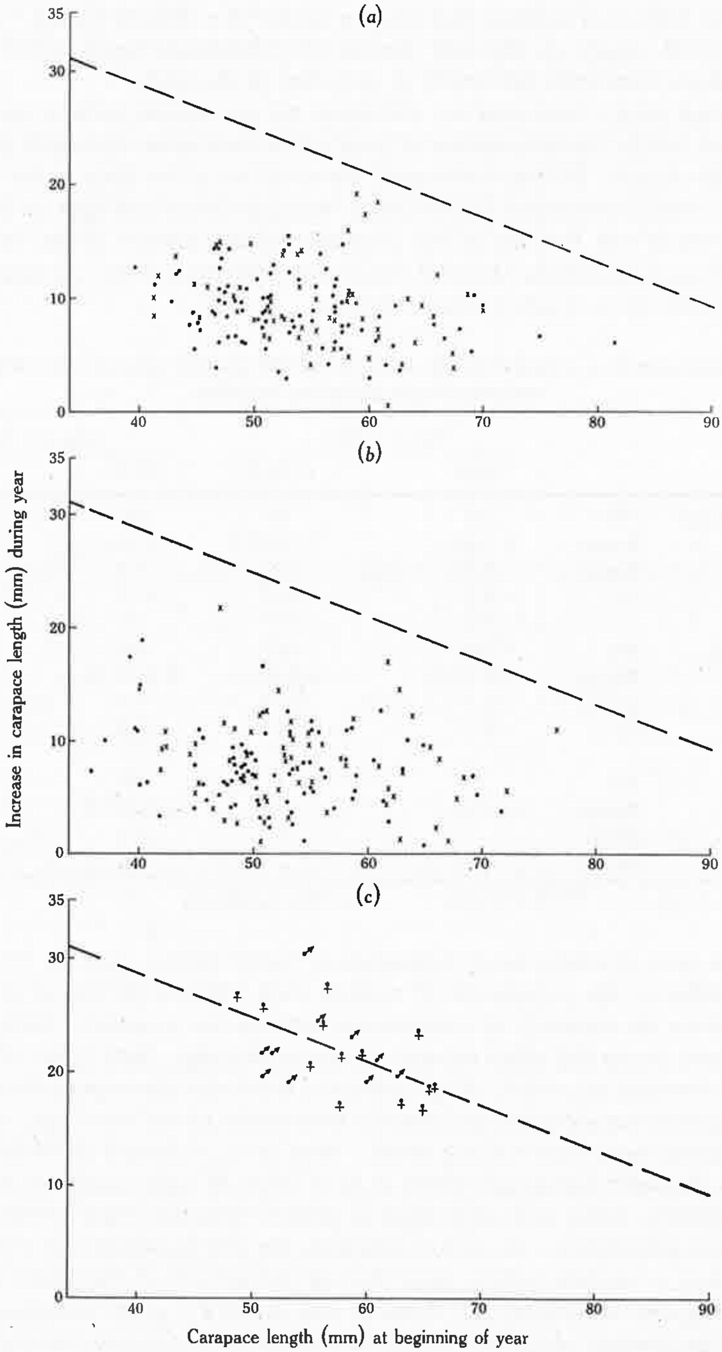

Fig. 6. Annual growth of tagged male (×) and female (●) western rock lobsters on (*a*) Garden Island and (*b*) Seven Mile Beach nursery reefs during 1971–74 compared with aquarium growth under near-optimal conditions (– – –). (*c*) Annual growth of 23 tagged western rock lobsters at Cliff Head in 1972 and 1973 compared with aquarium growth under near-optimal conditions (– – –).

algal covered reefs, it is unlikely that oxygen would be a limiting factor. This leaves insufficient food supply as the only known environmental factor which could be affecting the size increment per moult of juveniles on the reefs.

When developing a technique for indicating the nutritional state of western rock lobsters, Dall (1975) found evidence of poor nutritional state especially in juveniles at Seven Mile Beach. During underwater observations it has been noted repeatedly that these normally nocturnal feeders were foraging during daylight at Seven Mile Beach. Newman and Pollock (1974) have related the growth of the rock lobster *Jasus lalandii* to food supply, showing significant differences over a distance of a few kilometres (differing in depth in that instance).

Table 7. Annual growth in carapace length (mm) of marked juvenile western rock lobsters resident on nursery reefs at various localities

Locality		Age 3+ years			Age 4+ years		
		Male		Female	Male		Female
Seven Mile Beach	No.	44		58	26		41
	Range	1·1–21·7		2·0–18·9	1·2–16·9		0·8–12·6
	Mean	8·4	n.s.	8·2	7·7	n.s.	7·0
	s.e.	0·5		0·4	0·7		0·5
		***		***	*		***
Garden Island	No.	138		195	84		111
	Range	3·0–22·0		4·0–21·0	0·6–20·0		3·0–15·5
	Mean	11·3	n.s.	11·0	9·7	n.s.	9·0
	s.e.	0·3		0·2	0·4		0·3
					*		n.s.
Jurien Bay	No.	2		1	10		9
	Range	16·6–18·1		8·6	9·0–18·0		4·6–14·0
	Mean				12·4	*	8·7
	s.e.				1·0		1·0

* $0·01 < P < 0·05$. *** $P < 0·001$. n.s., Not significant.

From the data of single-moult increments it would appear that the level of food supply available to the population of western rock lobsters present at a particular time determines the intensity of competition between the juveniles. Where there is abundant food, or on the other extreme, a severe shortage, there is no difference in growth rate between the sexes. When there is a moderate shortage of food, juvenile females appear to compete less successfully than males of the same age, resulting in different growth rates between the sexes. Also in a moderate shortage of food, competition between age-groups (from 2 to 6 years of age) results in the smaller (younger) juveniles being more depressed in growth than the larger (older) members of the resident population. In such a situation, the size increment per moult of the older juveniles is actually greater than that of individuals of the same age reared under near-optimal conditions (cf. Table 2 and Table 1), again indicating that the larger juveniles compete more successfully for limited food resources and that retarded growth can be compensated to some extent in later years.

Where the food shortage was not too severe (e.g. at Garden Island) there were some fluctuations in growth from year to year as was recorded by Momot (1967) for the crayfish *Orconectes virilis*. However, no such variations were observed in the more severe conditions at Seven Mile Beach.

Further studies are needed of the food supply available to western rock lobsters. On the shallow reefs there may be cyclic changes in abundance of food species (or competitors) which are not directly related to fluctuations in density of juvenile rock lobsters. Also it is possible that some environmental factor other than food, population density, and temperature may be limiting growth rate at these localities.

In bringing together the available data presented and discussed above, Fig. 7 shows growth curves of western rock lobsters representing those at Seven Mile Beach, Garden Island, and the group raised under near-optimal conditions in aquaria.

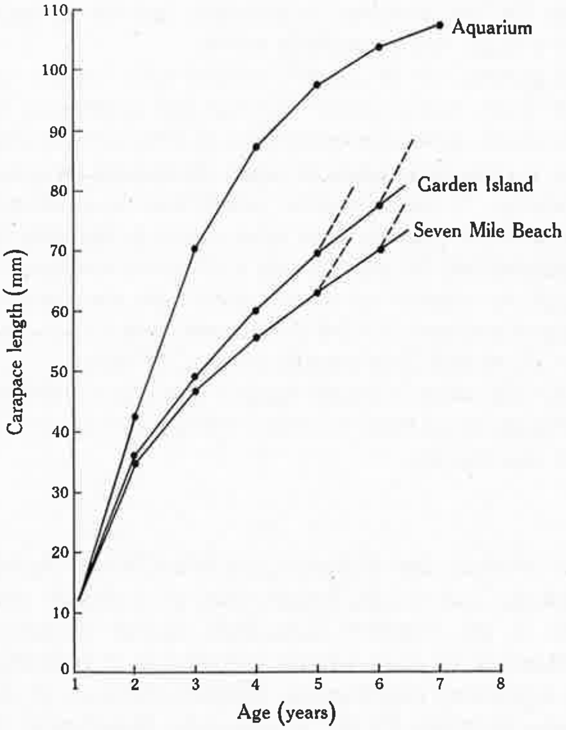

Fig. 7. Growth of juvenile western rock lobsters on nursery reefs and after migrating offshore (– – –) compared with those reared in an aquarium under near-optimal conditions.

From the modal sizes of those aged 2 years in the reef populations it would appear that during the first post-larval year growth in the shallow nursery areas was relatively good. Apparently these individuals were not in direct competition with older juveniles on the nursery reefs. From 2 to 6 years of age the residents of the nursery reefs were in direct competition with each other, depressing the growth rate of the younger juveniles more than the older ones. As soon as the juveniles moved out from the shallow nursery reefs (mainly at 5 or 6 years of age with an extreme range of 4–7 years) they were apparently freed from the intense competition for food so that growth rate accelerated. Although there are few data on growth in subsequent years, it is clear from the size composition of catches of adults taken at depths of 30–60 m that the asymptotic length and weight calculated for the aquarium group is commonly exceeded in the wild population where females of carapace length 140 mm (body weight 2·2 kg) and males of 180 mm (4·6 kg) are recorded.

Similar compensatory changes in growth rate have been recorded in other marine animals. Ursin (1963) showed that the members of the 1962 year-class of the Norway pout (*Gadus esmarki*) were smaller than those of the 1961 year-class at the times each entered the fishery, but after recruitment the 1962 year-class grew more rapidly, catching up to the 1961 year-class (at corresponding ages). Cooper and Uzmann (1971) found that deep-sea lobsters (*Homarus americanus*) grew at a faster rate, having a larger moult increment and higher moult frequency, than the smaller coastal lobsters.

Because a new set of environmental pressures operate on juveniles as soon as they emigrate from nursery reefs where growth has been retarded, enabling the growth rate to accelerate and compensate for the previous suppression, growth at such localities is not well represented by a single von Bertalanffy curve.

At one locality (Cliff Head) the growth rate of juvenile western rock lobsters on the nursery reefs equalled that of those reared under near-optimal conditions in aquaria. This was achieved in spite of sub-optimal temperatures on those reefs during winter months. Perhaps there was a synergistic effect of other favourable environmental factors operating at this locality. If those juveniles which were transplanted to Cliff Head had been severely retarded in growth when removed from the reefs at Seven Mile Beach, it might be suggested that the growth rate accelerated abnormally in making up the deficit. Although the number of observations from this locality was small, the growth rates of tagged residents at Cliff Head were within the same range as the growth rates of those which had been transferred to Cliff Head.

From the observations made at Cliff Head it would appear that the conditions needed to achieve the growth potential of juvenile western rock lobsters do occur in some parts of the distribution of this species.

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Breeding of *Panulirus longipes cygnus* George Under Natural and Controlled Conditions

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Abstract

Fertilization of eggs is external: the female does not need to be newly moulted to be mated. The incubation period of eggs (19–68 days) varied inversely with water temperature, being longest at 19°C and shortening towards an asymptote at 25°C.

Most adult females breed every year. When given abundant food, 77% of those breeding in aquaria at ambient temperature had two successive spawnings in a breeding season, whereas in a relatively crowded part of the natural population less than 12% of the breeding females spawned twice in a season. When held at a constant temperature of 25°C and given abundant food, adult females bred continuously, averaging six spawnings and three moults each year.

In the natural population, size at first breeding and mean size of breeding females did not vary with depth but differed from one locality to another. At the Abrolhos Islands where the present density of breeding stock is highest, adults appear to be stunted and fecundity is relatively low. This situation may have existed to some extent in other parts of the population before heavy commercial fishing of the past 20 years or more reduced the density of the breeding stock to present levels.

The operation of density-dependent regulation of fecundity in this population is discussed.

Introduction

There have been no comprehensive studies of breeding of the western rock lobster. Sheard (1962) and George (1958*a*) outlined the breeding cycle and indicated the seasons of mating, spawning and hatching. From larval surveys Chittleborough and Thomas (1969) indicated that hatching of larvae took place throughout the summer. In certain years hatching commenced earlier than usual, possibly due to an earlier rise of water temperature during spring stimulating earlier maturation of gonads. George (1958*a*) showed that at the offshore Abrolhos Islands breeding commenced at least 1 month earlier than along the coast.

The average size at first maturity of females throughout the population as a whole, based on the size at which 50% of the females were breeding, was given by George (1958*b*) as approximately 75 mm carapace length (when converted to presently used reference points on the carapace). Sheard (1954) recorded that at the Abrolhos Islands the smallest female with mature ovaries had a carapace length of 48·9 mm whilst the largest with immature ovaries measured 97·8 mm in carapace length.

A significant contribution on this subject was that of Morgan (1972) who measured the fecundity of female western rock lobsters of a wide range of sizes taken from various localities and at different stages of incubation of the eggs. He found that for females of a given size there was no difference in fecundity between localities, that the percentage of infertile eggs was low and independent of carapace length, and that there was only a small loss of eggs during incubation. A linear relation was established between female size (carapace length) and number of larvae produced from a single spawning.

Chittleborough (1974*a*) recorded some observations upon breeding of western rock lobsters held in laboratory aquaria. Those reared at a constant temperature of 25°C and given abundant food began breeding at 4·9–5·7 years of age (carapace length 97–106 mm) and thereafter bred repetitively.

Growth rate of juvenile western rock lobsters is inversely related to density (Chittleborough 1976) so the breeding capacity of the population might also show some density dependence through the sizes of adults and fecundity. The commercial fishery on this population has operated for over 30 years (Sheard 1962) and relatively high exploitation rates have been maintained for the past 20 years (Bowen and Chittleborough 1966) so that density-dependent breeding capacity should have had ample opportunity to operate if such a response occurs in this population. The evidence available on these aspects is examined and discussed in this paper.

Methods

In order to study the breeding cycle of individuals held at ambient temperature, a sample of adult rock lobsters taken by baited pots at a depth of 40 m was brought into aquaria. To ensure that there was no doubt as to breeding condition at the commencement of observations, the population was sampled in January and females carrying eggs (then in advanced stages of incubation) were selected. In each of three PVC tanks (180 by 90 cm, with water depth 29 cm) were placed five breeding females and two adult males, care being taken that at least one of the males was larger than any of the females, since Berry (1970) considered it unlikely that males (of *P. homarus*) are capable of copulating with females larger than themselves. Shelter was provided and the three groups were fed daily with mussels, abalone or fish, the quantity of food being adjusted so that there was some uneaten residue to be removed each day. Temperatures in the open-circuit seawater system were allowed to follow the seasonal cycle of incoming seawater, except that in winter temperatures were held at values previously recorded at a similar depth on the adjacent breeding grounds rather than being allowed to fall to the lower levels recorded at the near-shore intakes for the aquarium system. Lighting in the aquarium room was on a 12 h light : 12 h dark cycle to maintain a constant day length. Moulting, mating, spawning, and hatching were recorded for each animal over the next 15 months.

Another group of western rock lobsters reared in aquaria from puerulus larvae to maturity (Chittleborough 1974*a*) was held at the optimum temperature of 25°C (Chittleborough 1975) with shelter provided and feeding was as described above. Records were again kept of moulting and breeding.

The breeding condition of female western rock lobsters taken in the commercial catch was recorded at four localities each month by the field measuring team of the Western Australian Department of Fisheries and Wildlife. In contrast to the Norway lobster *Nephrops norvegicus* (Chapman *et al.* 1975) and the marron *Cherax tenuimanus* (Morrissy 1970), female western rock lobsters continue to forage actively while carrying eggs and enter pots readily (though returned to the water by fishermen). Catch sampling was grouped in 10-fathom (18-m) depth intervals, i.e. 0–18 m, 18–37 m, 37–55 m, and 55+ m. However, because the fishery is closed from 15 August to 15

November and during November and December it is almost exclusively within the shallower waters (the non-breeding zone), only sporadic information is available on breeding in the natural population during the spring. In the Southern Hemisphere, spring is taken as the period from 1 September to 30 November and summer from 1 December to 28 February.

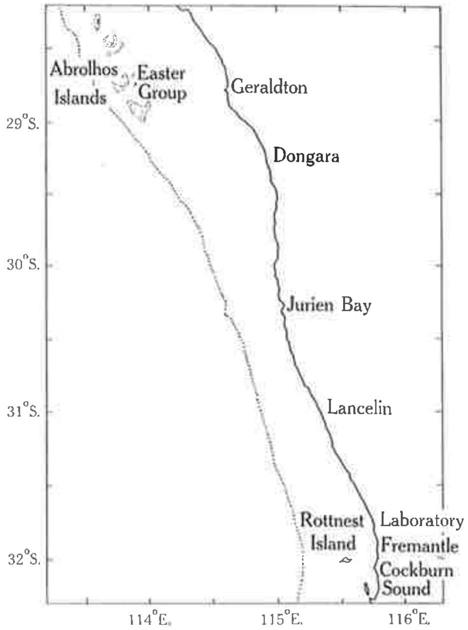

Fig. 1. Western rock lobster study area on the south-west coast of Australia.

At the Abrolhos Islands (a group of coral atolls on the outer part of the continental shelf as shown in Fig. 1) the fishing season does not open until 15 March so that throughout the spring and summer the breeding population could only be examined by sampling from a research vessel. During the summer of 1974–75 a tagging experiment was conducted to measure the proportion of adult females breeding more than once during a season. Early in December 1974, a total of 1793 breeding females were tagged and released using the tag developed by Chittleborough (1974*b*). Early in February 1975, 244 of these tagged females were retrapped, examined and released from the research vessel. After the opening of the fishing season on 15 March, a total of 140 tagged females (including some of those examined and released in February) were recaptured by fishermen. The data from this survey gave a comprehensive picture of the breeding activity for the period at that locality.

Breeding in Aquaria

At Ambient Temperature

Fig. 2 summarizes the subsequent breeding activity of the 15 female western rock lobsters brought into aquaria from the adjacent breeding grounds when carrying eggs in January 1974, and held at temperatures as close as possible to those recorded on that breeding ground.

During the following year only two (13%) of these adult females failed to breed. Both moulted in the autumn to the typical resting phase with very short setae (less than 2 mm) on the endopodites of the pleopods and remained in this condition at the next moult (275 and 309 days later). Though one female was the smallest of the group, the other was relatively large (Fig. 2) so that size (or age) does not appear to afford an explanation for the prolonged non-breeding period.

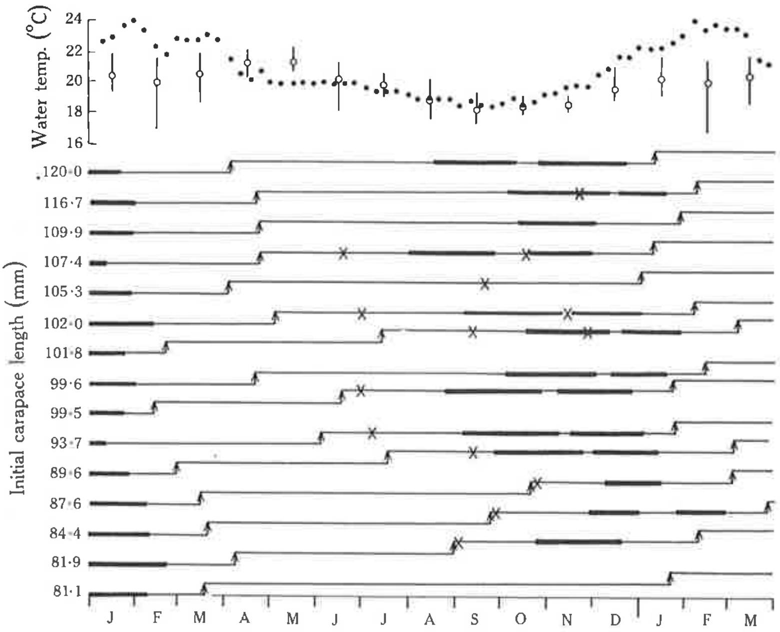

Fig. 2. Breeding cycles of 15 female western rock lobsters brought into aquaria in January 1974 and held at ambient sea temperature. ↑ Moult; × mating; ■ egg carrying; ● mean temperature (weekly) of seawater in aquaria; ○ mean temperature and range (monthly) recorded from 1971–73 at depth 50 m on adjacent breeding grounds.

Of the 13 females which bred in aquaria, 10 spawned twice in the following season and breeding commenced during the period of lowest temperature which was much earlier than was expected. George (1958*a*) showed that on the breeding grounds at 32°S. latitude spawning began in November and most egg laying occurred in December. Fig. 2 shows that in the aquarium group held at temperatures similar to those on the adjacent breeding grounds spawning began at the beginning of August, even before the seasonal minimum temperature occurred. Most larvae had hatched and breeding had terminated by the end of January, well before the maximum water temperature was reached.

Since these animals were lifted from the aquaria for close checking only once each week so that they would be disturbed as little as possible, the precise date of each mating was not always recorded. With external deposition of sperm packets on the sternum (Fig. 3), it was not necessary for the female to be newly moulted when mated. This characteristic of the genus *Panulirus* (external fertilization of eggs) contrasts with many other decapods where mating takes place when the female is newly moulted and the spermatozoa are lodged internally. In the aquarium-held western rock lobsters, successful mating occurred from 2 to 97 days after ecdysis. The cementing material extruded around the spermatophores darkened and hardened rapidly to the 'tar-spot' referred to by fishermen. This matrix affords a protective cover to the spermatophores similar to that described by Berry and Heydorn (1970) for *P. Homarus*. In the aquarium, western rock lobsters spawned (with successful fertilization of eggs) up to 69 days after mating.

Fig. 3. Ventral view of egg-bearing female western rock lobster showing 'tar-spot' (sperm packet) at rear of sternum and sub-chelate fifth walking legs.

During spawning the eggs were extruded from the ducts opening at the bases of the third walking legs. The sub-chelate dactyls of the fifth walking legs (Fig. 3) were used to break through the protective coat of the tar-spot, opening the spermatophores so that the eggs could be fertilized when being swept back to adhere to the elongated setae on the endopodites of the pleopods. As far as could be determined the sperm packets opened during spawning did not retain viable sperm, so that another mating was required if a second spawning followed the first. Although fresh sperm packets overlying eroded ones were not always distinguished, mating usually preceded the second spawning in the aquarium group. In some cases mating took place while the first batch of eggs was still being carried; in others the mating occurred during the few days between hatching and the subsequent egg laying.

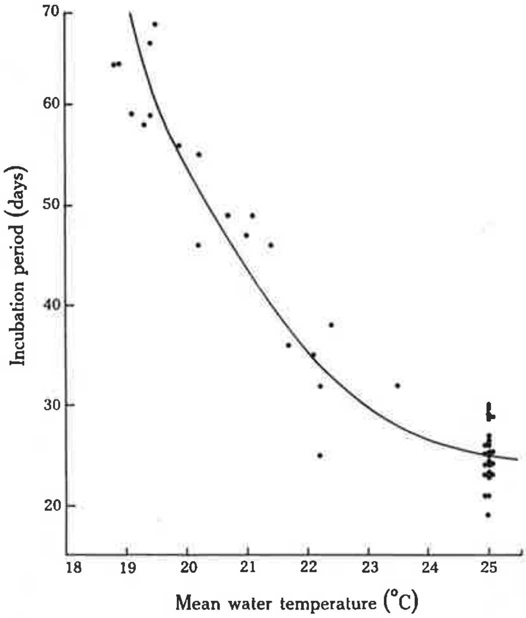

Fig. 4. Duration of incubation period for eggs of western rock lobsters held in aquaria at various temperatures. (Curve fitted by eye.)

The active male in one breeding tank produced sperm packets which did not cement very securely to the sterna of the females. Seven spawnings were noted for the females in this tank but in only one instance was a sperm packet observed on the sternum. The eggs from two of the spawnings were infertile and were lost after an incubation period of almost normal duration. In four cases the eggs were fertilized and hatching occurred even though sperm packets had not been observed on the sternum. Apparently the sperm packets were dislodged during or immediately after spawning which had occurred so soon after mating that the weekly check of breeding condition had not revealed the presence of sperm packets.

Two different types of moulting cycle were noted in these adult females. After a breeding season some moulted (in February or March) to a resting phase characterized by short setae (less than 2 mm) on the endopodites of the pleopods. Mating seldom occurred during this phase. These females then moulted again during winter or early spring (between June and October), the pleopods then having the long setae (10–15 mm) necessary for holding the eggs at the next spawning. Other females moulted only once between successive breeding seasons, the pleopods remaining setose at this moult so that there was no resting phase through an intermoult period. If moulting occurred soon (20–60 days) after the last eggs were hatched the cycle was of the first type (two moults in a year), whilst if the post-breeding moult was delayed (61–113 days) the cycle was of the second type.

When first brought into the aquaria, 46% of the breeding females went into the second type of cycle (a single moult between breeding seasons). However, after a year in captivity all continued with two moults between breeding seasons. The mean interval between hatching of eggs and subsequent moult was significantly greater ($0\cdot01 > P > 0\cdot001$) when breeding females were first brought into the aquaria (64 ± 19 days) than after these females had spent a year in captivity (36 ± 7 days). Possibly the daily feeding of aquarium-held adults improved their nutritional state sufficiently to elevate the moulting rate.

The duration of the incubation period varied inversely with water temperature (Fig. 4), incubation being extended very considerably at 19°C and shortening towards an asymptote at 25°C.

Fig. 5. Breeding cycles of three female western rock lobsters reared in aquaria from puerulus larval stage, held at a constant temperature of 25°C. ↑ Time of moult; × mating; ■ egg carrying.

At Near-optimum Temperature

A small group of three males and three females has been reared in aquaria under near-optimum conditions from the puerulus larval stage to maturity (Chittleborough 1974*a*). The seawater was maintained at a constant temperature of 25°C in order to maximize the growth rate (Chittleborough 1975, 1976).

Fig. 5 summarizes the breeding cycles of the three females after maturing at 4·9, 5·4, and 5·7 years of age respectively. Breeding cycles were continuous and regular under these conditions, there usually being two spawnings between successive moults. These females averaged three moults and six spawnings per year. Pleopods remained setose at each moult, the setae ranging from 11·6 to 16·2 mm long once breeding had commenced. Elongation of setae on the pleopods actually took place one to three moults (5–15 months) before the first spawning.

The sizes of the females represented in Fig. 5 were in the centre of the range of those represented in Fig. 2, but the ages of those brought in as breeding adults from the natural population cannot be assessed.

Breeding in the Natural Population

Breeding Season

In contrast to those western rock lobsters held in aquaria at a constant temperature of 25°C and with abundant food, breeding in the natural population is markedly seasonal, spawning occurring only in the spring and early summer. There may be some fluctuation from year to year in the time of spawning but there is little evidence of this because there is no fishing on the breeding grounds during spring. Chittleborough and Thomas (1969) and D. W. Rimmer (personal communication) found that the peak of hatching of larvae in summer varies in time from year to year (by as much as 4 weeks). The eggs carried by most females have hatched before mid-February. By mid-March (when the Abrolhos Islands fishing season opens) almost all of the adult females have moulted into the resting phase having non-setose pleopods.

Size at First Breeding

The presence (during the breeding season) of well-developed setae on the endopodites of pleopods has often been taken as an indicator of sexual maturity in female rock lobsters (George 1958*a*; Kensler 1967; Paterson 1969; Newman and Pollock 1971). However, as mentioned above, in young female western rock lobsters reared in aquaria the pleopods became setose 5–15 months before the first spawning.

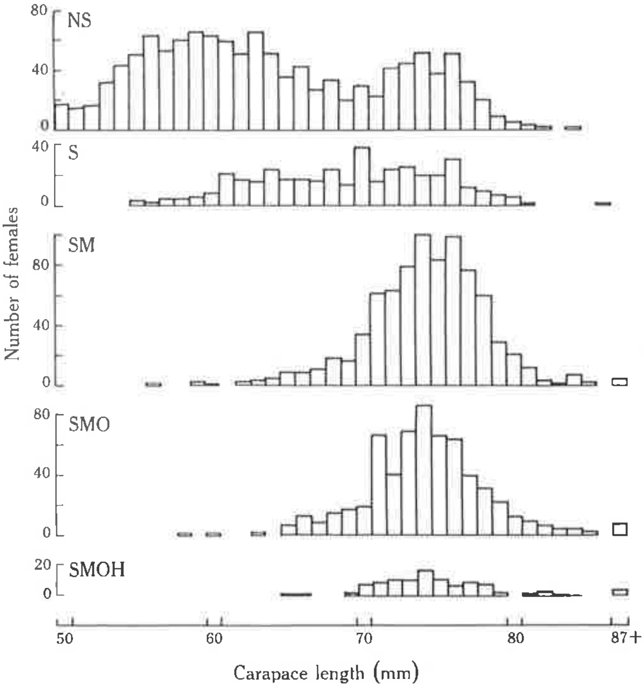

Fig. 6. Breeding condition of 3234 female western rock lobsters in the Easter Group, Abrolhos Islands, December 1974. NS, Non-setose endopodites of pleopods (non-breeding). S, Setose pleopods (unmated). SM, Setose pleopods; mated; sperm packet on sternum (not yet spawned). SMO, Ovulated (spawned); eggs carried under abdomen (eroded sperm packets). SMOH, Eggs hatched; few egg cases on setose pleopods, eroded sperm packets.

Sampling at the Easter Group of the Abrolhos Islands during the breeding season of 1974–75 showed that this also applies in the natural population. Fig. 6 shows that during December (the height of the breeding season at that locality) a wide range of size groups contained females having setose pleopods but as yet unmated. After tagging during December, 35 of these adolescent females were recaptured during the following February. Only two of these had been mated and none had spawned. Recaptures by fishermen late in March showed that almost all had moulted into the resting phase (non-setose pleopods) so that this group could not have reached maturity until the next spring.

A more reliable index of mean size at first breeding is the carapace length at which 50% of the females are breeding (spawned or mated or both), measured during the height of the breeding season. From the data shown in Fig. 6, groups SM, SMO, and SMOH have been combined and expressed as the percentage of the total catch of females for each 1-mm interval of carapace length. These percentages have then been plotted on probability paper (Fig. 7). As found by Wenner *et al.* (1974) for other species of Crustacea, this method enables a straight line to be fitted to the data from all but the larger size groups. As shown in Fig. 7, from intercepts of this line the mean and standard deviation can be derived for the carapace length of females at first breeding.

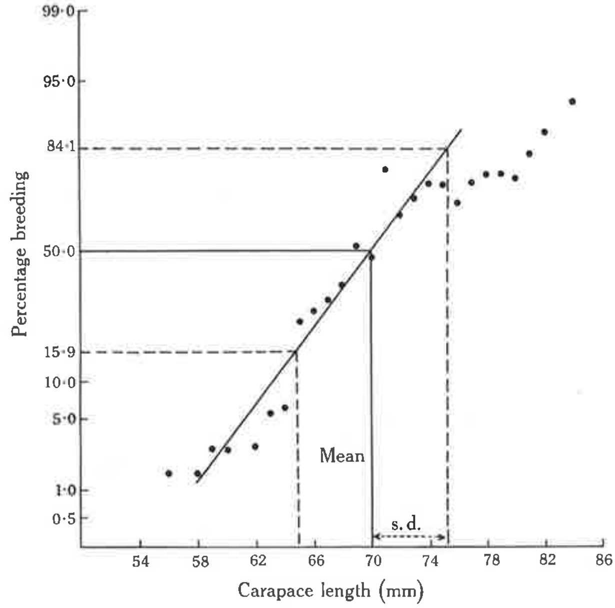

Fig. 7. Proportion breeding (SM, SMO, and SMOH of Fig. 6) in each size group from the Easter Group, Abrolhos Islands, in December 1974, plotted on probability paper.

The data represented in Figs 6 and 7 were obtained by sampling the population at the Abrolhos Islands across a depth range of 10–36 m. At that location (rising steeply on the outer part of the continental shelf) there appeared to be very little stratification of the western rock lobster population with depth, breeding adults being as well represented in the shallower waters as in deeper waters. However, along the mainland coast the population is stratified with depth as shown in the examples given in Figs 8*a*–8*c*. Virtually all of the females taken along the coast from depths of 0–18 m were immature, as were the majority of those taken from 18–37 m depth. Most of the breeding females were from depths greater than 37 m. Despite this stratification, Figs 8*a*–8*c* show that the size at first breeding did not vary with depth (apart from a consistent recording at Jurien Bay of little breeding at all of large females at depths exceeding 55 m).

By pooling the data from all depths at a given location along the mainland coast and obtaining the size at which 50% of the females were breeding (in the same manner as shown in Fig. 7), the mean size at first breeding was derived for females at each locality and year (Table 1). In recent years the size of females at first breeding has been much smaller at the Abrolhos Islands than elsewhere, and has been highest at the southern portion of the commercially fished coastal areas.

Age at First Breeding

From studies of growth of juvenile western rock lobsters on shallow reefs along the coast (Chittleborough 1976), it is known that most juveniles emigrate from these nursery reefs when 5–6 years of age. Even though the growth rate may then accelerate (as indicated from tag returns), a period of more than 1 year would be required to reach the mean size at first breeding recorded in Table 1 for recent years at localities such as Fremantle and Lancelin. At these localities the mean age at first breeding therefore would be 7–8 years of age.

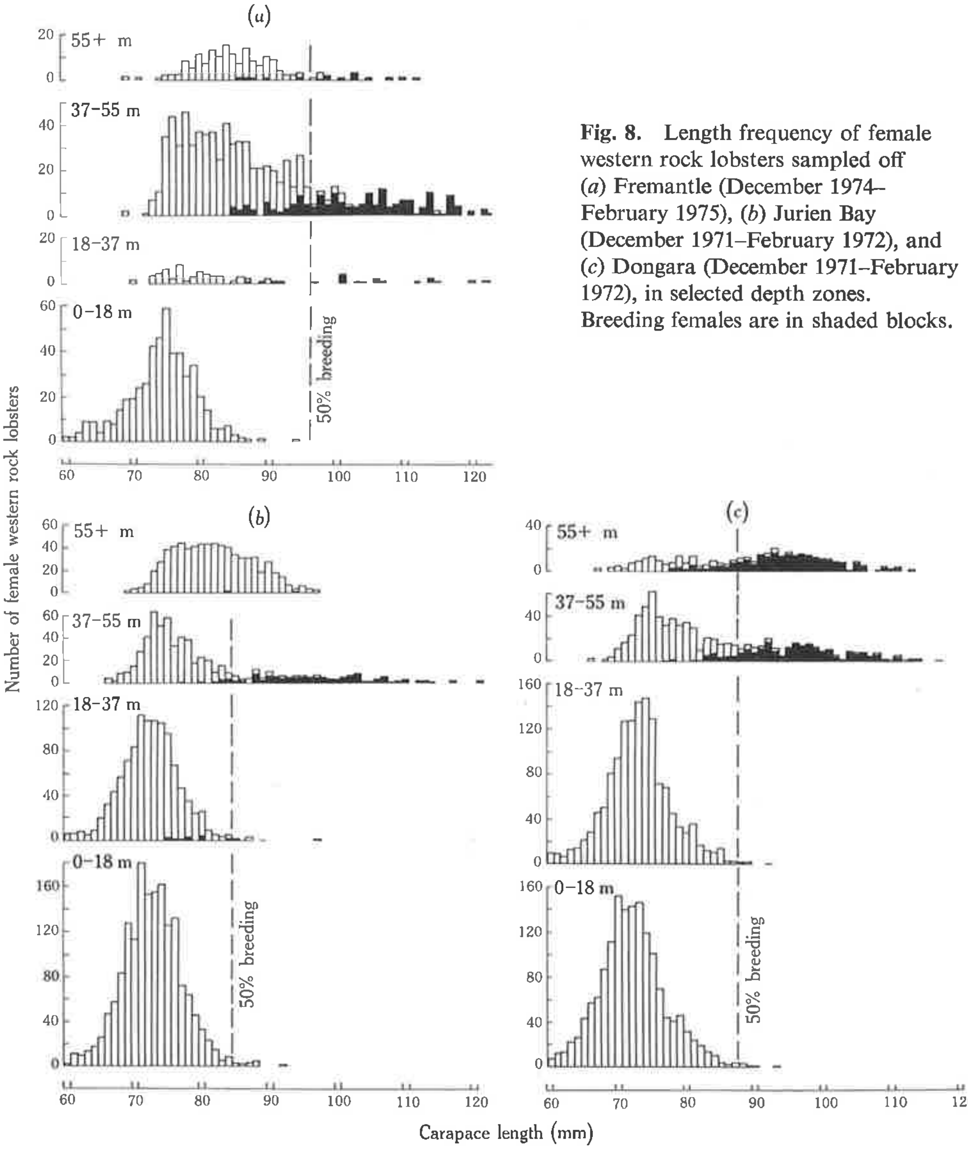

Fig. 8. Length frequency of female western rock lobsters sampled off (*a*) Fremantle (December 1974–February 1975), (*b*) Jurien Bay (December 1971–February 1972), and (*c*) Dongara (December 1971–February 1972), in selected depth zones. Breeding females are in shaded blocks.

At the Abrolhos Islands the mean size at first breeding is presently much smaller than elsewhere, but there is no evidence to suggest that breeding commences at an earlier age. On the contrary, from observations made in aquaria under controlled environmental conditions and from growth studies in other parts of the population (Chittleborough 1975, 1976 respectively) it is concluded that the growth rate of juvenile western rock lobsters in the Abrolhos Islands must be severely retarded.

Table 1. Size of females at first breeding and proportions of females breeding each summer (December–February) at various localities
CL, Carapace length

Locality	Smallest ♀ breeding, CL (mm)	CL at first breeding (mm)		Adult females[A]		
		Mean	s.d.	Total examined	Breeding	
					No.	%
Fremantle (32°03′S.)						
1954 (George 1958*a*)	74	77·2	3·5	—	—	—
1971–72	83	93·0	4·5	190	161	84·7
1972–73	83	96·2	5·4	341	231	67·7
1973–74	78	98·0	4·7	204	172	84·3
1974–75	85	96·2	5·7	182	165	90·7
Lancelin (31°01′S.)						
1972–73	82	95·7	5·3	53	45	84·9
1973–74	83	95·0	6·7	107	97	90·7
1974–75	86	96·4	6·0	190	170	89·5
Jurien Bay (30°17′S.)						
1971–72	67	86·0[B]	5·6	167	129	77·2[B]
1972–73	70	80·7[B,C]	7·6	53	36	67·9[B,C]
1973–74	71	91·0[B]	7·8	45	27	60·0[B]
1974–75	72	86·5[B]	4·2	97	78	80·4[B]
Dongara (29°15′S.)						
1971–72	77	87·4	3·9	475	418	88·0
1972–73	78	81·7[C]	3·2	225	211	93·8[C]
1973–74	—	—	—	—	—	—
1974–75	77	91·0	4·9	146	126	86·3
Abrolhos Islands (28°43′S.)						
Oct. 1964	59	64·9	4·6	1394	1152	82·6
Dec. 1974	56	70·1	5·3	1831	1339	73·1

[A] Those above mean length at first breeding.
[B] Excluding those taken at 55+ m depth.
[C] January data only.

Proportion of Adult Females Breeding each Season

Where sampling of the population was carried out during the breeding season, all those females above the mean length at first breeding were taken as adult and the percentage of these actually breeding was used to check whether only part of the adult stock breeds each year. The results shown in Table 1 indicate that the majority of the adult females breed each season and the proportion breeding has not declined in recent years. There remains the anomaly mentioned earlier (and shown in Fig. 8*b*) that few of the large females taken from deeper waters off Jurien Bay during the summer had been breeding. This has been noted in several successive years but as yet no satisfactory explanation can be offered. Cooper and Uzmann (1971) noted a similar phenomenon in large deep-sea lobsters *Homarus americanus* Milne Edwards, suggesting that in deep waters on the outer edge of the shelf, summer temperatures did not rise high enough for breeding to occur. There are insufficient data on temperature to enable this hypothesis to be tested in the case of the western rock lobster.

Frequency of Breeding during a Season

In the vicinity of Fremantle, if most female western rock lobsters spawned during December as observed by George (1958*a*) around 1954, there would be little prospect of females having more than one breeding cycle in a season, because at the water temperatures to which they were exposed most larvae would not have hatched until late January or early February.

Table 2. Monthly mean temperature of water in Cockburn Sound each spring (September–November) for 1960–75

Year	Monthly mean water temp. (°C)		
	Sept.	Oct.	Nov.
1960	16·4	17·8	18·9
1961	17·4	18·6	21·2
1962	17·1	17·5	20·1
1963	16·2	18·5	20·2
1964	16·8	17·2	19·1
1965	16·6	18·0	19·1
1966	15·9	17·0	20·1
1967	17·5	19·8	21·1
1968	15·2	16·6	18·5
1969	15·1	17·1	18·9
1970	16·2	17·8	18·9
1971	15·5	16·7	18·1
1972	17·3	18·3	20·5
1973	16·7	18·6	19·9
1974	17·8	18·6	20·3
1975	16·1	17·6	19·9
16-year mean	16·5	17·9	19·7

During the spring of 1975 an attempt was made to sample adult females in the fishing grounds near Rottnest Island. From 27 October to 6 November the very low catch rate (0·11 rock lobsters per pot-lift) indicated a very low density on these grounds. Only nine adult (mated) females were taken, but five of these were carrying orange eggs showing that spawning had occurred within 1 or 2 weeks. On this very limited evidence it would appear that in 1975 spawning was taking place at least 1 month earlier than recorded some 20 years ago in the same area. The water temperatures during the spring of 1975 were no higher than in previous years (Table 2). With a decline in population density and hence less competition for food there could be a trend towards earlier breeding similar to that found in the aquarium when adults held at ambient temperature were well fed (Fig. 2).

For those females spawning off Rottnest Island on 1 November 1975 at a temperature rising from close to 20°C, the incubation curve of Fig. 4 shows that larvae would hatch around 20 December. Using the results from aquaria at ambient temperature as a guide, there could be a second spawning 1 week later and with rising summer temperatures these eggs could be hatched by 1 February. This is about the time of hatching of eggs of the breeding females brought in from the adjacent breeding grounds in January 1974 (see Fig. 2). Although there is no direct evidence that females in the breeding grounds off Fremantle are now spawning twice in a season, the earlier spawning does make a second spawning possible.

With slightly higher water temperatures at the Abrolhos Islands there may be better prospects for females to breed twice in a season. In order to test this possibility, 1793 female rock lobsters were tagged and released in the Easter Group, Abrolhos Islands, early in December 1974. When each one was tagged the breeding condition was noted (as in Fig. 6) and for those carrying eggs a record was kept of whether eggs were freshly spawned (orange), developing (brown) or in advanced incubation (clear, with eyes visible). The Research Vessel *Flinders* returned to the same locality early in February, 52 days after the completion of tagging in December. As the water temperature at that time varied around 23°C, the incubation period for western rock lobster eggs would be close to 30 days (Fig. 4). From the breeding condition of tagged females recaptured in February, those which had spawned twice could usually be distinguished.

Table 3. Breeding condition of female western rock lobsters at the Easter Group, Abrolhos Islands, when tagged (December) and recaptured (February)

Condition at 5–12 December 1974		Condition at 2–7 February 1975						Total (December)
		S	SM	O	B	C	EH	
Setose pleopods (unmated)	S	33	2					35
Setose pleopods, mated	SM	1	75			1[A]	11	88
Eggs carried								
Orange	O		53	3[B]	1[B]		1[A]	58
Brown	B		5				7[B]	12
Clear (eyed)	C		4				1[B]	5
Eggs just hatched	EH		2				6[B]	8
Total (February)		34	141	3	1	1	26	206

[A] Possibly spawned twice in the season.

[B] Definitely spawned twice in the season.

The breeding condition of 206 individual females when tagged in December and recaptured the following February is summarized in Table 3. As discussed earlier, most of those having setose pleopods but not yet mated in December did not breed during that summer. These are taken to be maturing females which would begin breeding next season. Of 171 breeding females checked, only 10·5% could be confirmed as having spawned twice during the breeding season (with a possible maximum of 11·7%). This contrasts with the group held in aquaria at lower ambient temperature but given abundant food (Fig. 2) in which 66·7% bred twice in a season.

Mean Size and Fecundity of Breeding Stock

Table 4 shows the range and mean size of all breeding females sampled each breeding season at various localities. At the Abrolhos Islands the range and mean size was considerably less than for the breeding females from other parts of the population. This was to be expected owing to the much smaller size of females at first breeding, but in addition the size composition of breeding females at the Abrolhos Islands was less than elsewhere (cf. Figs 6 and 8).

Sizes of breeding females off Jurien Bay were slightly less than elsewhere along the coast. In recent years, the mean length of breeding females has been highest from the southern portions of the sampling range (where the mean size at first breeding is also highest). This is similar to the finding by Street (1969) that within the breeding stock of *Jasus edwardsii* Hutton in localities where the size at first maturity is larger, the greater maximum length is found.

To the mean length of breeding female western rock lobsters each summer has been applied the size–fecundity relationship established for this species by Morgan (1972). After allowing for egg losses during incubation (as measured by Morgan), Table 4 shows the estimated production of live larvae hatched per female at each locality. These estimates were made on the assumption of only one spawning per female. In recent years the production of larvae per female per spawning would appear to be highest in the southern part of the sampling range but there is some indication that this might not necessarily have been the case earlier in the exploitation of this population.

Table 4. Mean size and fecundity of female breeding stock sampled from catches each summer (December–February)

Locality	Breeding females[A]			Estimated production of live larvae hatched per female
	No. examined	Carapace length (mm) Range	Mean	
Fremantle				
1954 (George 1958*a*)	67	74–110[B]	89·6	282 800
1971–72	180	83–134	106·5	441 100
1972–73	250	83–143	110·0	473 800
1973–74	205	78–133	107·5	450 400
1974–75	222	85–127	103·5	413 000
Lancelin				
1972–73	71	82–120	100·7	386 800
1973–74	103	83–130	107·5	450 400
1974–75	189	86–135	108·0	455 100
Jurien Bay				
1971–72	235	67–127	88·4	271 700
1972–73	105	70–118	83·1	222 100
1973–74	73	71–121	89·2	279 200
1974–75	141	72–122	91·7	302 600
Dongara				
1971–72	484	77–117	95·5	338 100
1972–73	226	78–123	94·3	326 900
1973–74	—	—	—	—
1974–75	156	77–118	97·3	355 000
Abrolhos Islands				
Oct. 1964	1275	59–88	71·5	113 500
Dec. 1974	1547	56–107	74·3	139 700

[A] Mated, with or without spawning.

[B] Mid-points of 2·5-mm class intervals.

Individually, the mean fecundity is lowest for that portion of the population at the Abrolhos Islands, but the relative contribution of larvae by females at this locality should not be under-rated. The breeding stock at the Abrolhos Islands is less vulnerable to fishing pressure, partly because the fishery there is not opened until after the breeding season, but more importantly because the majority of the breeding females are below the legal minimum length (carapace length 76 mm). The present density of the breeding stock at the Abrolhos Islands may be considerably higher than elsewhere along the coast. At the Easter Group, Abrolhos Islands, in December 1974, using commercial-type pots on an area regularly fished commercially, the research vessel took 1548 breeding females in a total of 406 pot-lifts, giving a mean catch rate of 3·81 breeding females per pot-lift. In January and February 1975 the mean catch of breeding females per pot-lift by fishermen operating from Geraldton to Fremantle at depths of 37–55 m was 0·14 (G. R. Morgan, personal communication). On this basis, the present density of breeding stock in the Abrolhos Islands might be as much as 27 times the mean density of breeding stock elsewhere. Even allowing for the fact that the mean fecundity of females at the Abrolhos Islands is presently approximately one-third of that of females at other localities, it is possible that a major part of the coastal recruitment is derived from the breeding stock in the Abrolhos Islands.

Discussion

Fecundity is a product of two variables—breeding frequency and number of young produced per breeding cycle. Each of these may respond independently to changes in environmental pressures.

Considering first the frequency of breeding in the female western rock lobster: from the relative ease with which the number of spawnings per year can be increased under aquarium conditions, it would appear that in the natural population females do not achieve their full potential in breeding rate. Temperature is clearly one of the environmental factors involved, the annual cycle of water temperature confining breeding cycles to the spring and summer. But the aquarium experiments indicate that other factors exert a considerable effect upon the frequency of breeding. The most important of these may be the nutritional state of the individuals. When supplied with abundant food, adult females in aquaria increased their frequency of breeding despite seasonally low temperatures similar to those in the adjacent breeding grounds.

In those natural populations where density is high (and the state of nutrition apparently poor), most adult females (at least 88%) spawn only once per year despite the fact that water temperature is high enough to permit breeding through the greater part of the year. Where the density of the population has been lowered very considerably by intensive fishing, the decreased competition for food may increase the nutritional state of adult females to levels where a higher proportion spawn more than once in a breeding season.

Several members of the genus *Panulirus* have been shown to be capable of spawning more than once during a breeding season. Ino (1950) suggested that a considerable number of female *P. japonicus* spawn twice in a season. Sutcliffe (1953), Williams (1965) and Buesa (1969) recorded that in *P. argus* some females have two spawnings in a season without a moult between the two breeding cycles. Berry (1971) found that female *P. homarus* bred repetitively with up to four breeding cycles in a year. *P. longipes cygnus* has now been shown to have a similar capability.

The other determinant of fecundity, the number of young produced per breeding cycle, is directly related to the size of the female and this in turn reflects the growth rate occurring at that locality.

Data collected in recent years show considerable differences from one location to another in both the size at first breeding and also in the sizes attained by breeding females. A superficial appraisal of the evidence (Tables 1 and 4) might lead one to suggest that this conforms to the widely held theory (Bradstock 1950; Sutcliffe 1951; Street 1969) that the size at first maturity (and hence maximum size) is inversely related to mean water temperature. However, apart from the fact that the females off Jurien Bay do not fit into such a trend, the mean annual surface temperature recorded by Sheard (1962) at the Abrolhos Islands (21°C) is scarcely different from that off Dongara (20·5°C), and the difference is insufficient to account for the very considerable difference in size at maturity. The mean annual temperature is 20°C at Jurien Bay and 19·8°C off Fremantle. In addition, the size at first breeding recorded by Chittleborough (1974*a*) for those reared at 25°C in aquaria was higher than the sizes recorded in recent years in the southern portion of the range (Table 1), again conflicting with the hypothesis of an inverse relation between water temperature and size at maturity.

As the western rock lobster population stands today, where the density of the breeding stock is highest (at the Abrolhos Islands) retarded growth has apparently resulted in the small size at first breeding and the low mean size of all breeding females, with a correspondingly low production of larvae from each spawning. At other localities where the present density is lower much, both the size at first breeding and the size composition of the adult female population are higher, so that more young are produced per individual breeding cycle. In these areas the density of the breeding stock would have been much higher 20 or 30 years ago, before commercial exploitation reached high levels. At that time the breeding population along the coast may have been similar in structure to that now observed at the Abrolhos Islands. As the accumulated breeding stock (relatively stunted in growth) was thinned out, the growth rate of those remaining may have improved with consequent increase in size at first breeding and larger size of adults. This would then explain why there has been so little indication of a change in size composition of catches over this period. With an increase in size composition there would have been a corresponding improvement in mean fecundity.

Apart from the somewhat circumstantial evidence of aquarium experiments and the present contrast in breeding at the Abrolhos Islands with that at coastal localities, there are very few data from the early years at the opening of this fishery to test the hypothesis that the breeding stock along the coast may then have had a lower size at first breeding and a lower mean fecundity than recorded in recent years. The only available data are those given by George (1958*a*) and as shown in Tables 1 and 4, these support the hypothesis. The data quoted were obtained from adult western rock lobsters taken on shallow reefs at Rottnest Island and it needs to be confirmed that these would be typical of the general locality. The western end of Rottnest Island protrudes across the depth contours where the breeding stock is generally located so that here the breeding population extends into shallow waters in the same way as described at the Abrolhos Islands. As discussed earlier, there is no evidence that the size at first breeding varies with depth. But in addition to the data collected at this specific locality, George (1958*b*) also examined breeding females at a variety of localities during the period 1953–56 and he concluded that for the population as a whole the mean carapace length of females at first breeding was then close to 75 mm. Table 1 shows that this is much smaller than the present mean size at first breeding at coastal localities.

There may then be two ways in which density-dependent regulation of fecundity may operate in the western rock lobster population. At high population density the individuals in the breeding stock may be stunted, resulting in low numbers of eggs per spawning (due to the direct relation between size of female and number of eggs carried) and only one spawning per breeding season. As the population density decreases improved growth rate could produce larger females which in turn carry more eggs per spawning. Also as the state of nutrition of breeding females improves, a higher proportion of the females may have a second spawning during the breeding season.

Although it is suggested that the breeding stock of the western rock lobster may be experiencing such changes in fecundity as a result of fishing pressure, it is not possible to assess whether the total production of larvae has actually increased, maintained its earlier level, or declined. However, the studies of Chittleborough and Phillips (1975) show that settlement of final-stage larvae along the shallow coastal reefs is generally still in excess of the holding capacity of these nursery areas, confirming that the breeding stock is still producing sufficient larvae to maintain the level of recruitment in most areas.

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Contribution No. 18

NATURAL REGULATION OF THE POPULATION OF *Panulirus longipes cygnus* GEORGE AND RESPONSES TO FISHING PRESSURE

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Abstract

Larval, juvenile and adult phases are each of considerable duration and occupy generally distinct habitats with independent environmental pressures. Within the breeding stock, fecundity is highly density dependent. In crowded localities growth rate is retarded, females are smaller at first breeding and do not attain large size. With a direct relation between size of animal and number of eggs per spawning, mean fecundity is low. In addition, most females in a crowded stock spawn only once per season. When the breeding stock is at low density, size at first breeding and upper size range of breeding females are much higher resulting in more eggs per spawning. Also when food is abundant a higher proportion of females spawn twice in a season. Mean fecundity is then considerably increased.

During the relatively long (10 months) larval phase it is possible that the low levels of zooplankton off the west coast of Australia impose density dependent mortality upon rock lobster larvae. However, the relative success of settlement of larvae along the coast may be determined more by density independent factors such as fluctuations in oceanic

circulation in this region.

Juveniles spending 4-5 years on shallow nursery reefs have been shown to be subject to density dependent mortality (and lowered growth rate), apparently due mainly to limitations in availability of food on coastal reefs. Because settlement of larvae is generally in excess of the carrying capacity of the nursery reefs, it is at the juvenile phase that the level of recruitment is mainly determined.

The intensive fishery of the past 20 years has reduced the breeding stock but has not (as yet) impaired recruitment to the fishable stock.

INTRODUCTION

The western rock lobster occurs on the west coast of Australia from about 22°S to 34°S, being most abundant between 28°S and 32°S. The fishery on this population developed from a total catch of 272 tonnes in 1944-45 to 9707 tonnes in 1962-63 (Bowen and Chittleborough, 1966). Since 1963 the fishing units (both boats and pots) have been strictly limited by regulation, annual catch fluctuating between 6780 tonnes and 9892 tonnes.

Larval, juvenile, and adult phases are of considerable duration and generally occupy distinct habitats with environmental pressures acting independently on each. Thus density dependent regulation of population size might operate at any one of these phases. The limiting factors applying at each phase of the life cycle are reviewed in order to determine the points at which natural regulation is achieved at present, and if possible to assess whether the environmental pressures have been altered by the high exploitation rate.

The western rock lobster is predominantly carnivorous at each phase of the life cycle. Newly hatched larvae in aquaria will accept brine shrimp larvae. Late stage phyllosoma take larger planktonic crustacea such as euphausiids (Chittleborough and Thomas 1969). Juveniles show a preference for molluscs but will accept various teleosts, crabs, and sea urchins (Chittleborough 1975). Quantities of coralline algae have been found occasionally in the foregut of juveniles on nursery reefs but these algae are not considered to be an important energy source for this species.

ADULT PHASE

Most of the adult population lives in a broad strip of the continental shelf at depths of 30 to 90 m. Where off-shore islands rise steeply from depths of 30 m or more, and also where the coastal zone (0 to 30 m) is very narrow, breeding adults may be found on shallow reefs together with the juveniles. Fishermen sometimes locate patches of western rock lobsters in deep water (to 160 m), but only a low proportion of the total stock lives deeper than 90 m.

Chittleborough (1976a) has shown that there are two ways in which density dependent regulation of fecundity may operate on adult western rock lobsters. When given abundant food, 77 per cent of females breeding in aquaria at ambient temperature had two successive spawnings in a breeding season, whereas in a relatively crowded part of the natural population less than 12 per cent of the breeding females spawned twice in a season. The number of eggs produced per spawning has been shown (Morgan 1972) to be related linearly to size (carapace length) which in turn is density determined through growth rate. In that part of the population where the present density of the breeding stock is highest, the mean size at first breeding is smallest, adults are generally stunted, and fecundity correspondingly low. At other localities where the density is much lower, both size at first breeding and the size composition of adult females are higher so that more larvae are produced per individual breeding cycle. There is some indication that before commercial exploitation had reduced the density of the breeding stock in these latter areas, the size at first spawning may have been less and hence individual fecundity lower than now observed.

There is then the potential for natural regulation of larval numbers produced by this population, the conclusion being that as the density of the breeding stock is lowered, the state of nutrition of each female is improved, resulting in a higher growth rate and increased fecundity. The question then arises whether such changes in fecundity have been carried through to have any impact on eventual recruitment to the breeding stock.

LARVAL PHASE

Larvae hatch from late November through to February. Newly hatched larvae rise towards the surface and are carried off the shelf probably by offshore surface wind drift (Chittleborough and Thomas, 1969). By May the main concentration of western rock lobster larvae is 500 km offshore, some being found over 1200 km from the coast. Final stage larvae return to settle along the coast, the peak of settlement occurring during the following spring and early summer (September through December) (Chittleborough and Phillips, 1975).

During the 9 to 11 months of oceanic planktonic life, the larvae are subject to very high mortality. An index of larvae mortality may be obtained by comparing the density of newly hatched larvae on the shelf during summer with the density of final stage larvae returning across the shelf in the spring. The mean density of stage I phyllosoma from 44 stations on the shelf near the centre of the range during summer was approximately 143,000 per ha of sea surface (Rimmer, unpublished data). The mean density of puerulus larvae in the same area of the shelf during the spring was approximately 60 per ha (Phillips, Rimmer and Reid, 1976). Recognising that these are rather crude estimates owing to the patchiness of newly hatched larvae and the assumption that first and final stage larvae are equally vulnerable to the sampling gear, these data indicate that total mortality of larvae may be over 99.9 per cent. High larval mortality is expected in highly fecund species, but actual measurements are sparse in the literature.

Little is known of the causes of mortality in western rock lobster larvae. Shortages of planktonic food may restrict both growth and survival, the oceanic waters off the western coast of Australia having very low productivity. Surface waters in this region are deficient in dissolved nutrients (Kirkwood, 1967, Rochford 1962, 1967, 1969) and also very low in zooplankton (Tranter, 1962). Tranter compares this area with the Sargasso Sea as extreme examples of oligotrophic water where both primary production and standing crop of zooplankton are at their lowest. In such a situation predation of rock lobster larvae may be severe but observations are very few (see Chittleborough and Thomas, 1969). While starvation and predation could both cause density - dependent mortality of rock lobster larvae, fluctuations from year to year in survival of larvae have not been related to initial density or to variation in productivity of surface waters.

A major source of larval losses may be the variability of water circulation in this region causing fluctuations in the numbers returned close enough to the continental shelf for successful settlement. This part of larvae mortality would be independent of larval density. Adverse currents may cause the greatest losses of these widely ranging but poorly mobile larvae.

JUVENILE PHASE

After the puerulus larvae have returned across the shelf to settle along the coast, juveniles spend the next 4 to 5 years gathered on shallow "nursery" reefs. During this phase the juveniles are not exposed to much commercial fishing pressure, being below the legal minimum length (carapace 76 mm). In earlier years there was some traffic in undersize rock lobsters but with more rigid inspection and the introduction of escape gaps in pots (Bowen, 1971), pre-recruits are generally well protected.

Rather more detailed information is available upon density, growth and survival of juveniles (Chittleborough 1970, 1976b; Chittleborough and Phillips, 1975) than for the other phases of the life cycle. Both growth and natural mortality of juveniles are density-dependent. On the more crowded nursery reefs it would appear that food and shelter are both limiting factors. As a result, year classes strong at the time of larval settlement are exposed to higher mortality rates and tend to spend longer on nursery reefs (due to retarded growth) so that recruitment to the fishery is much the same as that resulting from a more modest settlement of puerulus larvae. Only a particularly weak year class can be traced through from the time of larval settlement to recruitment into the fishery (Chittleborough and Phillips, 1975).

Although direct measurements of the availability of food have not yet been made, the productivity of nursery reefs may well be very limited in this region where input of nutrients from oceanic waters is particularly low and run-off from the land is also low. If western rock lobsters are near the top of the food web of the reef community, the gain in weight of the juveniles in a year can be taken as an index of the productivity of these nursery reefs. Some preliminary calculations have been made, assuming that the study reef is a closed system for the whole of the year (no migration) and that the mean natural mortality rate measured from January to August applies for the whole year to each of the age groups within the population.

In the Garden Island test area (32°10'S) where the density of Table 1 juvenile rock lobsters is relatively low (Table 1) the biomass (standing crop) was similar to that found by Allen (1951) in the Horokiwi Stream in New Zealand. However, production (year's weight increase) on the rock lobster reef was very much lower than that recorded by Allen for the trout and was even less than the low production of North American lakes (Mann 1965). The very low ratio of production to standing crop may indicate that the reef community at Garden Island was energy limited.

In the test area at Seven Mile Beach (29°08'S) where the density of young rock lobsters is very high, a more severe situation exists. The initial biomass was very high but production was negative, i.e. there appeared to be a considerable loss in biomass during the year. Tagging has shown that this loss was not due to dispersion. One can only conclude that these reefs were heavily overstocked so that the total energy required for metabolic activity was in excess of the energy available through the food chain. The rock lobster population might then have drawn upon itself (i.e. cannibalism) to make up part of the deficiency, resulting in a decline in biomass.

Though steps need to be taken to refine these crude assessments they do indicate that productivity of the coastal reefs is low and that settlement of rock lobster larvae may well exceed the carrying capacity (in terms of energy production) of these reefs.

An indication of the relative success of recruitment of juveniles to the fishable stock can be obtained from the success of the "white" fishery at the beginning of each season. From the opening of the season on November 15, the fishing of the next six weeks is concentrated just off the shallow coastal reefs to catch the newly moulted "white" phase adolescents which are then moving offshore (George 1958). Chittleborough and Phillips (1975) estimated that from one half to two thirds of the rock lobsters taken at this time have just left the shallow nursery reefs.

g. 1 Figure 1 shows that the total fishing effort expended in the coastal "white" fishery (November and December) has been relatively constant since 1961. Then fluctuations in total catch at this time during the past 15 years may reflect variations in annual recruitment. One limitation here is that while occasional catches from deep water (over 80 m) have been deleted from the records since 1968, it has not been possible to do this for earlier "white" seasons. Thus the total catch for coastal "white" seasons prior to 1968 might be over-estimated by as much as 20 per cent. Another factor possibly affecting the level of catches shown in Figure 1 could be fluctuations in catchability due to differences in water temperature (Morgan 1974).

Though there are these limitations in using the total catch in the "white" season as an index of recruitment, the catch data in Figure 1 indicate that the range of variability in recruitment for this population is not particularly high in comparison with other marine populations, being within the range of less than an order of magnitude. This range was cited by Cushing (1974) as typical for demersal fish populations having high fecundity, relatively slow growth rate, and high indices of density dependence.

DISCUSSION

The western rock lobster population shows a good deal of flexibility in responding to changes in environmental pressures (either natural or man-made). But because each phase of the life cycle is stressed separately, a favourable response within one phase is not necessarily to the benefit of the population as a whole. For example, a thinning out of the adult stock (by heavy exploitation) leads to an increase in mean fecundity but this has no impact upon the eventual recruitment to the fishable stock while settlement of larvae upon the nursery reefs continues to be in excess of the carrying capacity of these reefs.

Least is known of the environmental pressures operating upon the oceanic larval phase, but for management purposes this is of less importance since the greater part of larval mortality may be independent of density and also may be little affected (at present) by man-made pressures.

In the centre of the coastal range, larval settlement continues to be in excess of the carrying capacity of the nursery reefs, density dependent effects on mortality and growth rate maintaining relatively stable recruitment to the fishery. Nearer the periphery of the coastal distribution, low points in fluctuations of larval settlement are more likely to result in depressed recruitment, the peaks in settlement again being removed during the four to five years spent on nursery reefs by the juveniles. The density-dependent mortality of juveniles represents a wastage of pre-recruits which raises prospects for some form of intervention as discussed by Chittleborough (1970) and Chittleborough and Phillips (1975).

Though recruitment continues to be adequate at present, the most vulnerable point in the management of this heavily exploited population is the adult stock. It is not known whether the size of the breeding stock continues to decline, and if so, at what level there will be an impairment of recruitment to the fishery.

With low productivity on coastal reefs being the major limiting factor responsible for regulating the population and maintaining relatively steady recruitment, the western rock lobster conforms well to the generalisation by Chekunova (1972) that members of the *Palinuridae* are mainly confined to well balanced communities in hydrologically stable waters without upwelling and associated fluctuations in productivity. They usually occupy complex trophic systems. Such biocenoses are characterised by a moderate or low productivity.

In such a community the western rock lobster population maintains maximum use of food resources by saturation settlement of final stage larvae throughout a considerable portion of its coastal range.

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TABLE 1

ESTIMATES OF BIOMASS OF WESTERN ROCK LOBSTERS ON NURSERY REEFS AND PRODUCTION (GROWTH vs. MORTALITY) IN ONE YEAR

A. GARDEN ISLAND 1974

	JANUARY			DECEMBER				Net prodn. kg/ha/yr
Age Group yrs.	Density no./ha.	Mean wt. gm	Biomass kg/ha	Survival	Density no./ha.	Mean wt. gm	Biomass kg/ha	
2+	404	45.3	18.3	.678	274	109.8	30.1	
3+	1200	109.8	131.8	.678	813	196.6	159.8	
4+	505	196.6	99.3	.678	342	299.7	102.5	
5+	155	345.0	53.5	.678	105	465.2	48.8	
TOTAL	2264		302.9		1534		341.2	+38.3

B. SEVEN MILE BEACH 1974

2+	10775	40.1	432.1	.464	5000	97.5	487.5	
3+	9700	97.5	945.8	.464	4500	161.2	725.4	
4+	3400	161.2	548.1	.464	1580	236.5	373.7	
5+	900	305.9	275.3	.464	420	402.2	168.9	
TOTAL	24775		2201.3		11500		1755.5	-445.8

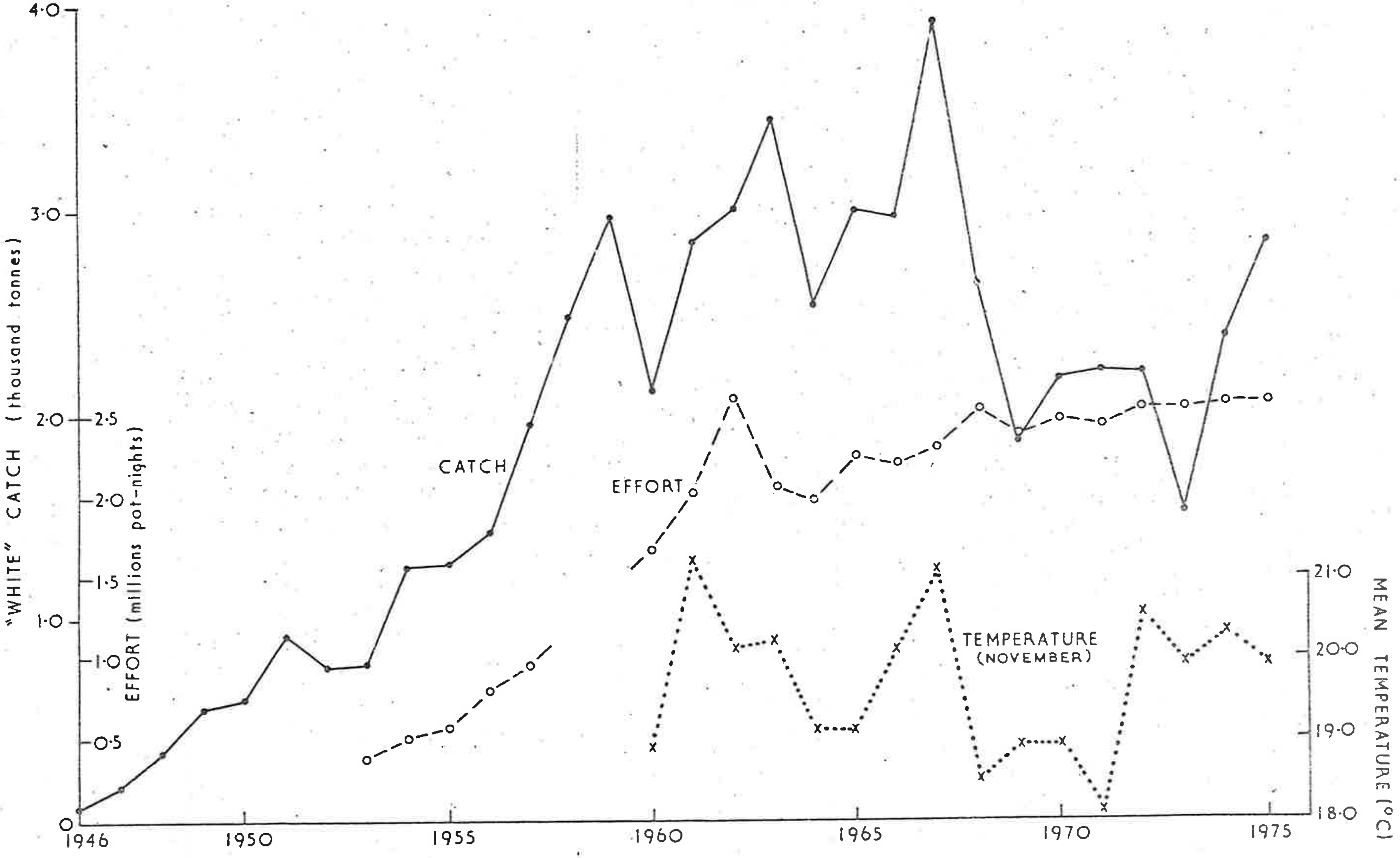

Fig. 1. The "white" fishery (Nov. 15-Dec. 31) on the western rock lobster in each of the past 30 years. Total catch ● ; Fishing effort o ; Nov. mean water temp. at 32^{o}S X.

Paper 27

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SOUTHERN RIGHT WHALE IN AUSTRALIAN WATERS

The importance of the southern right whale (*Balaena australis* Desmoulins) in the early settlement of Australia is not generally recognised. The pursuit of this whale brought many of the first non-convict settlers to Australian (especially Tasmanian) shores. In fact a whaler carried the first settlers to Tasmania in 1803, and for the next forty years this new colony was mainly engaged in the pursuit of the southern right whale, as reviewed by Dakin (WHALEMEN ADVENTURERS, 1934).

This species was once abundant along the southern coast of Australia and around New Zealand between May and October, the females entering sheltered bays to calve and nurse their young (Dieffenbach, TRAVELS IN NEW ZEALAND, I, 1843; Pearson, Pap. and Proc. Roy. Soc. Tasmania, 1935: 166–167, 1936). At this phase they were relatively easily killed, beached and stripped of blubber and baleen. Thus "bay whaling" commenced in Tasmania and rapidly extended along the southern coast of Australia and to New Zealand, reaching a peak about 1840. Dakin records that in 1841 there were 35 bay whaling stations in Tasmania alone. As well as the bay whaling stations, many whaling ships ranged along the southern coast of Australia taking southern right whales and sperm whales. It is said that in 1841 there were nearly 300 American and French whalers along the southern coast of Australia.

The practice of indiscriminately killing the calves as well as females about to calve, was criticised as early as 1832 by Hay (see Dakin) and in 1839 by Dieffenbach (1843), both warning that the southern right whale would soon be exterminated in this way. This theory was quickly verified as bay whaling began to decline from 1840, and by 1843 southern right whales were becoming scarce in this area. The pursuit of this species soon ceased and the sperm whale was hunted more intensively.

The damage thus done to this stock of southern right whales was so severe that in the present century (in spite of full protection) individuals of this species have been rarely sighted along the Australian coast: in fact I can find no such published records. Wood Jones (THE MAMMALS OF SOUTH AUSTRALIA III, 1925) noted that in the previous fifty years no specimens had been stranded or captured along this coast.

However, on August 2, 1955, a pair of southern right whales were sighted in Frenchman's Bay, close to Albany, Western Australia. Due to the co-operation of the manager of the Cheynes Beach Whaling Company (which operates a whaling station at Frenchman's Bay), I was able to observe these whales at close quarters from a launch.

This pair consisted of a female approximately 55 feet, and a calf 18 to 20 feet, in length. Both appeared to be healthy. They spent the greater part of the day in shallow water (2–3 fathoms) close to shore. When approached they were lying quietly at the surface, then moved leisurely (at about 2 knots) along the shallows, making no effort to reach deeper water. On three occasions the 36 foot launch scraped over the female's back, but apart from a temporary increase in speed, this did not appear to unduly disturb these whales.

The calf kept very close to the cow, which turned the calf by physical contact: this sometimes resulted in the calf sliding over the cow's back, almost clear of the water. The callosity upon the snout, known as the 'bonnet' was well developed in the calf as well as in the cow.

While following these whales, the intervals between successive blows were recorded for the adult. The first set of intervals were 35, 120, 63, 42, 28, 128, 50, 43, 20 seconds, and in a further series of blows the intervals were 120, 75, 180, 40, 50 and 20 seconds. There appeared to be a fairly regular periodicity in the blows; one after an interval of two minutes or more was followed by briefer soundings of down to 20 seconds, followed by another longer sounding of two to three minutes. After a brief sounding the blow was not very distinct, but after a longer sounding the blow had the characteristic V-shaped appearance figured by Matthews (Discovery Repts., 17: 169–182, 1938). The calf tended to blow more frequently than the cow, but sometimes sounded for up to two minutes.

In view of the apparent rarity of the southern right whale in spite of long protection, it is hoped that any further sightings will be fully recorded.—R. G. CHITTLEBOROUGH, C.S.I.R.O., Division of Fisheries, ℅ *University of W.A., Nedlands, Western Australia.*

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Paper 28

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Balaenoptera Brydei Olsen on the West Coast of Australia

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In October 1958 three whales, tentatively classed by gunners as sei whales, *Balaenoptera borealis* Lesson, were taken off Shark Bay, Western Australia. From the general description of their external appearance and limited biometrical data obtained, these whales could have been either sei whales or Bryde's whales, *Balaenoptera brydei* Olsen.

However, photographs (Plate 1) showed features typical of Bryde's whales. On the ventral surface a grey band extended «across the belly in front of the umbilicus» as described by Olsen (1913) for Bryde's whales. Anterior baleen plates (Plate 1) were white and the remainder were greyish black. Mr. K. Godfrey, who examined these whales, noted that the bristles of baleen were coarse and grey in colour. Examination of samples of baleen collected (Plate 2) showed them to be typical of the Bryde's whale as illustrated by Olsen and also by Omura, Nishimotu and Fujino (1952) for what must be regarded as the Bryde's whale taken off the Bonin Islands.

Details of the three whales taken on the west coast of Australia are given in Table 1. One of the females was sexually mature and the male must also be regarded as mature since Omura (1950) showed that in the Bonin Island area males having a testis weight of over 1 kg. were mature. However, both mature individuals were far smaller than mature specimens recorded by Omura or by Olsen from the Bonin Islands and the South African coast respectively.

Another difference found in the specimens taken on the west coast of Australia was that the baleen plates were considerably shorter than those found by Olsen in Bryde's whales from the South African coast. This might merely be related to the smaller overall size of the Australian individuals, but there is also a marked difference in the ratio baleen width to baleen length. Olsen found a mean of 45 per cent. for this value (four individuals) whereas in the three Australian specimens the mean was 73 per cent., similar to the values obtained for the baleen of fin and blue whales (Mackintosh and Wheeler 1929).

All three whales were feeding when killed, the stomachs containing large quantities of the anchovy *Engraulis australis* Shaw, the majority of which were less than 5 cm. in length, a few reaching 9 cm. In addition there were several partially digested fish, approximately 10 cm. long which may have been young mackerel.

Olsen suggests that as this species is not dependent on small crustacea for food, it does not migrate. His records show that at least some few Bryde's whales can be found on the South African coast at all times of the year, but there is some indication that larger numbers are present in that region during autumn and winter.

The ear plugs of the three specimens from the Australian coast contained laminations similar to (but smaller than) those present in the ear plugs of the larger species of baleen whales. If the laminations are directly related to the seasonal migrations of the larger whales, this might be indirect evidence that Bryde's whales also undergo seasonal migrations. On the other hand, if the laminations in the larger whales are the result of fluctuations of food

Plate I.

Plate 1. Bryde's whales taken off the west coast of Australia

supply, the presence of similar laminations in Bryde's whales might be taken to indicate seasonal variations in availability of suitable food (small fish) in the area frequented by a non-migratory species of whale.

The traces obtained from samples of baleen plates collected from these whales show relatively abrupt increases in thickness along the plates, but the material is too limited to enable proper interpretation of these.

This species has been recorded previously only from the coasts of Africa and the Bonin Islands, although recently Harrison and Jamuh (1958) mentioned that specimens had been stranded on the

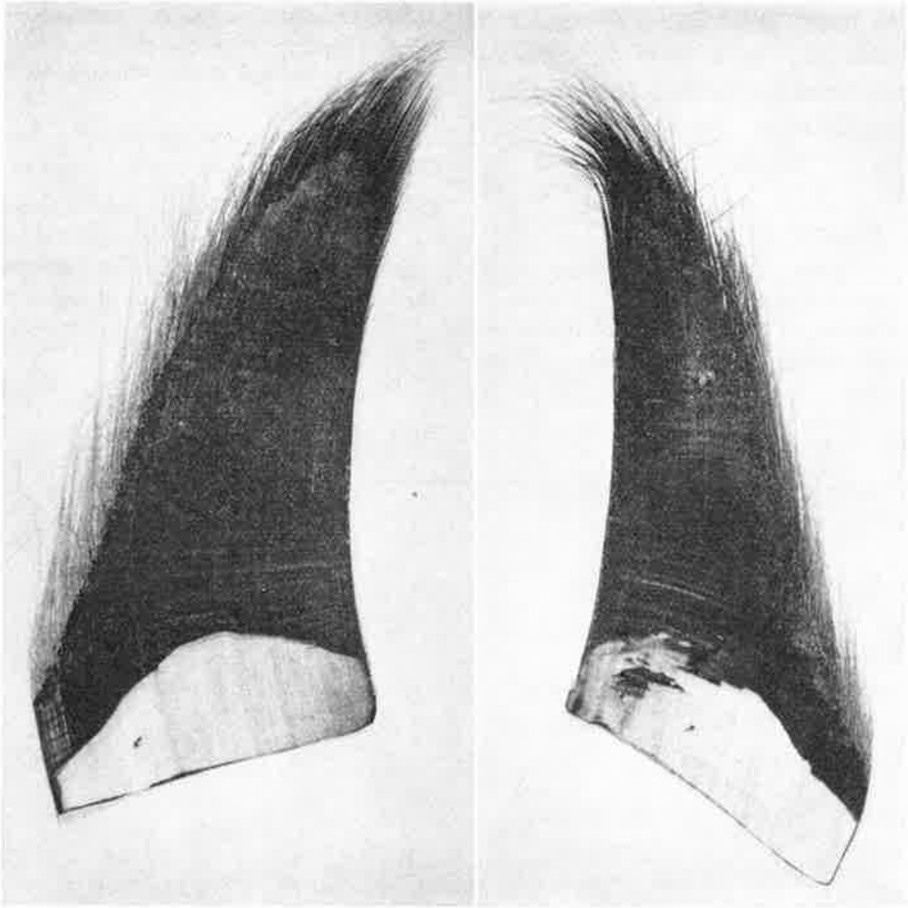

Plate II.

Plate 2. Baleen from Bryde's whales. Left: No. 1A. Right: No. 2A

Table 1.
Bryde's Whales taken on the West Coast of Australia.

	1A	2A	3A
Date killed	10.10.58	10.10.58	12.10.58
Position	24°35'S. 112°58' E.	25°03'S. 112°55' E.	24°35'S. 112°58'E.
Sex	Female	Female	Male
Length	34 ft. 8 in.	38 ft. 6 in.	36 ft. 10 in.
Ovaries:—			
Diameter largest follicle	4 mm.	12 mm.	—
Number corpora albicantia	0	11	—
Testis weights	—	—	2.7, 2.6 kg.
Ear plugs:—			
Length of core (mid line)	13.5 mm.	14.5 mm.	14.0 mm.
Laminations	7—9, poorly defined	21, most sharply defined, but poor at base	15, fairly well defined
Baleen: longest plates			
Length to gum line (excluding bristles)	21.5 cm.	21.5 cm.	23.5 cm.
Width at base	15 cm.	16 cm.	17.5 cm.
Width/length	69.8 %	74.4 %	74.5 %
External parasites	none present	none present	none present

coast of Borneo. The capture of Bryde's whales in Australian waters extends the known distribution of the species. It has been suggested (Ruud 1952) that Bryde's whales occur in the warmer regions of all oceans.

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A/S Handelstrykkeriet - Sandefjord

Paper 29

COMMONWEALTH SCIENTIFIC AND INDUSTRIAL RESEARCH ORGANIZATION

DIVISION of FISHERIES and OCEANOGRAPHY

Report No. 58

THE TROPICAL ROCK LOBSTER *Panulirus ornatus* (Fabr.) AS A RESOURCE IN TORRES STRAIT

R. G. Chittleborough

Marine Laboratory
Cronulla, Sydney
1974

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THE TROPICAL ROCK LOBSTER *PANULIRUS ORNATUS* (FABR.) AS A RESOURCE IN TORRES STRAIT

by R.G. Chittleborough

INTRODUCTION

A fishery upon *P. ornatus* has developed in Torres Strait since 1969. Although relatively small in comparison with major rock lobster fisheries elsewhere, the catches represent an important source of income to the islanders of this region. Some concern has been felt that reefs may be overfished if the rock lobster fishery continues to expand. For these reasons, the Department of Aboriginal Affairs asked the Division of Fisheries and Oceanography, CSIRO, for advice on the resource and its management.

As it has not been possible to mount a large-scale survey, the following should be regarded as an assessment of the problem, with suggestions for immediate management and also for useful lines of further study of this resource.

THE FISHERY

During the past three years, the annual production of rock lobster tails from Torres Strait has been in the range of 150,000 - 200,000 lb. This represents approximately 395,000 -525~~0~~,000 lb live weight of catch. Practically the entire catch is *P. ornatus*. Some 10-12 vessels (32-55 ft in length) equipped with freezers are engaged in rock lobster fishing. The larger of these are converted pearling luggers. Several dinghies operate from each vessel, rock lobsters being taken from coral outcrops by shallow diving (mainly 1-3 m) and spearing. Tails are removed and the rock lobster heads left around the reef. When dinghies return to the vessel, each man's catch is counted and weighed, the tails are washed, the digestive tract removed and the tails placed in plastic bags and frozen.

Most of the catch is returned to Thursday Island where there are three processing and freezing plants. The current price paid by processors is $1-30 to $1-40 per lb of tails. The Queensland Department of Aboriginal and Island Affairs has ruled that a minimum of $0-75 per lb be paid to those employed in diving. Processors have imposed a minimum tail weight of 4 oz.

Less is known of the segment of the fishery which is based at Daru. It is understood that one of the three processors there exported 41,169 lb of *P. ornatus* tails in the ten months from July 1970 to April 1971. The three rock lobster operators based at Daru employ an unknown number of divers and canoes which spread over some of the same reefs fished by those from Thursday Island.

THE RESOURCE

P. ornatus favours moderately turbid water (Pyne 1970) and is practically the only species of rock lobster on the shallow reefs of Torres Strait. Further to the east of Torres Strait and Cape York, as the clearer waters of the Barrier Reef are approached, *P. ornatus* is replaced by *P. versicolor* and an occasional *P. longipes femoristriga*.

Because *P. ornatus* does not enter baited traps, methods applied in assessing western rock lobster resources, e.g. the catch per pot-night as an index of abundance (Bowen and Chittleborough 1966), or mark-recapture estimates of population density (Chittleborough 1970) cannot be applied directly to the rock lobster population of Torres Strait. Some measure of fishing effort (however crude) is required in order to check whether there have been any trends in the catch per unit effort during the brief history of this fishery.

Upon examining records kept of the operations of several fishing vessels, it was possible to determine the weight of rock lobster tails taken per man per day's fishing during successive cruises (Tables 1-3). This affords an index of abundance of rock lobsters on the shallow reefs, bearing in mind that the crew on a vessel may change in time (varying skill) and that weather conditions have considerable influence on the effectiveness of the fishing effort.

Although the catch rates shown in Tables 1-3 are highly variable, there is a general pattern of higher catches per man per day from April or May through to September and lower values from October to March. For vessel "M", the peak catch rates were lower in the most recent season, mainly due to replacement of part of the crew with less experienced divers, and perhaps also to more fishing on the eastern side of Cape York than in the centre of Torres Strait.

Both vessels "E" and "Y" obtained highest catch rates during the most recent season, having located good concentrations of rock lobsters on reefs near Mobiag Island, an area fished consistently in previous years without spectacular results. An experienced rock lobster fisherman commented that the reefs near Mobiag Island afford plenty of cover but in previous years held only moderate numbers of rock lobsters, most of which were relatively small, yet this season the sizes have improved as well as the numbers.

TABLE 1

CATCHES OF *P. ORNATUS* BY VESSEL "M" IN RECENT YEARS

(Trips of approx. 2 weeks cycling round Mobiag, Warrior Reef, East Coast of Cape York in turn. Mainly east coast during past 12 months.)

Date (returned)	No. of men	No. of dinghies	Total catch		Mean wt tails taken per man per day*	Mean tail wt (lb) per rock lobster
			Number	Tail wt (lb)		
Apr. 30, 1971	10	5	3517	2520	21.0	.717
May 25, 1971	9	5	4168	3452	32.0	.828
June 22, 1971	8	4	3328	2658	27.7	.799
July 23, 1971	9	5	4713	3870	35.8	.821
Aug. 11, 1971	9	5		3881	35.9	
Aug. 25, 1971	11	6	2648	2113	16.0	.798
Sept. 20, 1971	12	6	3709	3159	21.9	.852
Oct. 1-10, 1971	11	6	1668	1220	13.9	.731
Oct. 20-Nov. 2, 1971	10	5	1854	1360	11.3	.734
Dec. 10, 1971	9	5	2254	1907	17.7	.846
Dec. 16, 1971) Jan. 20, 1972)	10	5	2011	1632	11.7	.812
Feb. 11, 1972	10	5	3001	2352	19.6	.784
Mar. 10, 1972	10	5		2129	17.7	
Apr. 12, 1972	10	5		800	6.7	
Apr. 28, 1972	10	5	1734	1536	12.8	.886
May 25, 1972	10	5		2544	21.2	
June 26, 1972	8	4		2325	24.2	
July 24, 1972	7	4	2141	1818	21.6	.849
Aug. 18, 1972	7	4	1914	2450	29.2	1.280
Sept. 15, 1972	8	4	2215	3143	32.7	1.419
Sept. 30-Oct. 7, 1972	8	4	635	718	15.0	1.131
Nov. 10, 1972	9	5	874	1116	10.3	1.277
Dec. 19, 1972	8	4	1439	843	8.8	.586
Jan. 29, 1973	7			1160	14.0	
Feb. 28, 1973	5			713	11.9	
Apr. 11, 1973	6+		964	952	13.2	.988
May 4, 1973	5++	3	1239	1324	22.1	1.069
May 19, 1973	4	2	1010	942	19.6	.933
June 13, 1973	5	3	709	619	10.3	.873

* Assuming 12 days fishing each trip unless otherwise recorded

\+ Two men and four boys on this trip

++ Three men and two boys

TABLE 2

CATCHES OF *P. ORNATUS* IN TORRES ST. BY VESSEL "E" IN RECENT YEARS

Period	Days worked	No. of men	Catch tail wt (lb)	Mean wt tails per man per day
Mar. 21-25, 1969	3	7(?)	293	14.0
Oct. 19-28, 1971	8	5	470	11.8
Nov. 1-20, 1971	18	3	941	17.4
Nov. 26-Dec. 13, 1971	16	4	973	15.2
Jan. 30-Feb. 16, 1972	16	2	705	22.0
Mar. 25-Apr. 7, 1972	12	4	991	26.4
Apr. 21-May 9, 1972	17	5	1011	11.9
May 17-June 1, 1972	14	7	1378	14.1
June 7-19, 1972	11	6	1094	16.6
June 24-Jul. 7, 1972	12	6	1393	19.3
July 11-23, 1972	11	7	1353	17.6
Aug. 16-20, 1972	3	6	510	28.3
Aug. 23-Sept. 6, 1972	13	6	810	10.4
Sept. 13-Oct. 1, 1972	17	6	777	7.6
Oct. 8-25, 1972	16	6	1160	12.2
Nov. 1-15, 1972	13	6	787	10.1
Nov. 19-Dec. 9, 1972	19	6	863	7.6
Dec. 13-21, 1972	7	6	431	10.3
Feb. 20-Mar. 2, 1973	9	6	494	9.2
Mar. 7-20, 1973	12	6	1066	14.8
Mar. 24-Apr. 4, 1973	10	6	1301	21.7
Apr. 8-20, 1973	11	6	1363	20.7
Apr. 26-May 4, 1973	7	6	1078	25.7
May 9-20, 1973	10	6	1394	23.2
May 24-31, 1973	6	6	1387	38.5
June 9-15, 1973	5	6	1562	52.1

TABLE 3

CATCHES OF *P. ORNATUS* IN TORRES ST. BY VESSEL "Y" IN RECENT YEARS

Period	Days worked	No. of men	Catch tail wt (lb)	Mean wt tails per man per day
Mar. 21-26, 1969	4	9	442	12.3
June 7-22, 1972	14	10	1671	11.9
June 26-Jul. 9, 1972	12	9	1700	15.7
Jul. 12-31, 1972	18	7	1698	13.5
Aug. 2-8, 1972	5	6	390	13.0
Aug. 15-27, 1972	11	7	893	11.6
Aug. 30-Sept. 14, 1972	14	8	623	5.6
Sept. 16-21, 1972	4	8	116	3.6
Oct. 24-Nov. 8, 1972	14	9	916	7.3
-Dec. 20, 1972	?	8	82	?
Feb. 10-16, 1973	5	7	450	12.8
Feb. 21-Mar. 4, 1973	10	9	1563	17.4
Mar. 8-18, 1973	9	9	1563	19.3
Mar. 24-Apr. 1, 1973	7	10	1737	24.8
Apr. 8-16, 1973	7	8	1539	27.5
Apr. 21-May 2, 1973	10	8	1237	15.5
May 5-14, 1973	8	9	2023	28.1
May 19-30, 1973	10	8	2472	30.9
June 3-10, 1973	6	13	2212	28.4

One fishing vessel (Table 1) recorded the total number of rock lobsters taken as well as the total weight of tails so the mean tail weight per animal gives an index of the average size of rock lobster for each trip. The increase in mean weight for most of the catches in the last year may be due in part to this boat operating more often on the eastern side of Cape York.

The seasonal cycle in abundance on the reefs in Torres Strait is the opposite of that recorded by Pyne (1970) for Yule Island where *P. ornatus* is taken during the N.W. monsoon season (November-April). This may reflect different methods of fishing in the two areas rather than differences in behaviour patterns of the rock lobsters.

With the aim of comparing the relative abundance and size composition of rock lobster populations on reefs having different histories of exploitation, the fishing vessel *Manahiki* was chartered for two weeks in September, 1973. The main reefs chosen were Dungeness Reef which has been well fished for at least five years, and Wapa Reef which has had less fishing because of high turbidity and strong tidal flow. The five fishermen were encouraged to operate in their usual way except that rock lobsters were brought intact to the *Manahiki* where the CSIRO observer (H. Kirkman) measured and examined each before processing took place. The total time each dinghy was away fishing was recorded, giving a much more precise measure of fishing effort than available previously.

Table 4 shows the catch per unit effort each day, both as the number of rock lobsters taken per man hour and also as tail weight per man hour. Although the data are insufficient for adequate statistical comparison, catch rates on the less fished reef (Wapa Reef) were similar to those on more regularly fished reefs (Dungeness and Warrior Reefs). Fluctuations in turbidity and tidal stream from day to day and from one reef to another made it impossible to compare the relative abundance of rock lobsters on the different reefs. It should be noted that another vessel from Thursday Island and four canoes from Daru were fishing Wapa Reef at that time.

While variability in skills of individual divers is not important when comparing catch rates of the whole group moving from one reef to another, the former is important when comparing operations of different boats or long term changes in catch rate on one boat. Table 4B shows that two of the fishermen on *Manahiki* had much greater skill and experience than the other three.

The sex ratio of catches taken in September 1973 consistently favoured males (Table 4), similar to that recorded by V. Wells in the same area in December 1959 (33 per cent females). The mean tail weight per rock lobster did not vary significantly from one reef to another and was similar to that of catches in the same area more than two years earlier (compare Tables 4 and 1). This indicates that there has not been a decline in size composition as a result of fishing operations.

TABLE 4A

SUMMARY OF CATCH AND EFFORT BY *MANAHIKI* OPERATING ON *P. ORNATUS* IN TORRES ST. DURING SEPTEMBER 1973

Date		Reef	Effort		Catch		Catch per unit effort		Mean tail wt (lb)	♀ %
			No. men*	Total hrs +	No.	Tail wt (lb)	No. per man hour	Tail wt per man hour		
Sept. 9	p.m.	Dungeness R.	5	21½	219	154	10.2	7.2	.703	41.1
10	a.m.	Dungeness R.	5	23½	116	85	4.9	3.6	.733	32.2
	p.m.	"	5	21	140	104	6.7	5.0	.743	38.3
11	a.m.	Dungeness R.	5	20	117	97	5.9	4.9	.829)	32.1
	p.m.	"	5	16-3/4	130	97	7.8	5.8	.746)	
12	a.m.	Dungeness R.	5	19	76	62	4.0	3.3	.816)	32.1
	p.m.	"	5	14	115	91	8.2	6.5	.791)	
Sept. 13		Wapa R.	5	31¼	198	164	6.3	5.3	.828	43.6
14	a.m.	Wapa R.	5	7½	80	55	10.7	7.3	.688)	39.6
	p.m.	"	5	32½	266	210	8.2	6.5	.789)	
Sept. 15	a.m.	Warrior R.	5	20	41	31	2.1	1.6	.756)	35.6
	p.m.	"	5	15	62	49	4.1	3.3	.790)	
16	a.m.	3m N. Makai	5	7½	46	32	6.1	4.3	.696	34.8
	p.m.	Warrior R. (S)	5	20	151	119	7.6	6.0	.788	39.2
17	a.m.	Warrior Is.	5	10	93	72	9.3	7.2	.774	38.0
	p.m.	1½m S. Dungeness Is.	5	11-3/4	20	16	1.7	1.4	.800	
18		Dungeness R.	5.	25	147	111	5.9	4.4	.755	26.1
					2017	1549			.768	

* Not including CSIRO observer   + Includes travel to and from *Manahiki*

TABLE 4B

SUMMARY OF THE 10 DAYS FISHING BY INDIVIDUALS ON *MANAHIKI*, SEPT. 1973

Fisherman	No. rock lobsters per hr		Total tail wt per day	
	Range	Mean	Range	Mean
A	6.6 - 16.0	11.4	27 - 71	53.5
S	2.6 - 25.1	10.7	13 - 93	48.3
M	2.0 - 5.8	3.7	9 - 31	16.1
H	1.6 - 4.0	3.0	8 - 37	14.7
B[+]	1.6 - 6.1	3.5	5 - 36	16.8

[+] Including some taken by CSIRO observer.

TABLE 5

SIZE COMPOSITION OF *P. ORNATUS* TAKEN FROM TORRES ST. REEFS IN SEPTEMBER 1973 *(MANAHIKI)*

Carapace length (mm)	Dungeness R.		Dungeness R.*		Wapa R.		Warrior R. *et al.*	
	♂	♀	♂	♀	♂	♀	♂	♀
<62	1	1	0	0	0	0	0	0
63	0	0	2	0	0	0	0	0
64	0	0	0	0	0	0	0	0
65	4	2	0	0	0	0	0	0
66	0	1	0	1	1	0	0	0
67	1	0	1	0	0	0	0	0
68	1	0	0	1	0	0	0	1
69	2	2	0	0	1	0	0	0
70	3	2	0	2	1	2	1	1
71	1	2	0	0	1	1	2	0
72	5	1	0	0	1	1	1	1
73	3	2	1	3	3	4	0	0
74	3	3	1	0	3	3	1	1
75	2	5	1	0	2	0	2	1
76	4	8	1	1	3	3	1	2
77	9	5	3	1	1	2	2	4
78	4	4	1	0	2	3	0	0
79	10	7	1	1	8	3	5	3
80	14	8	1	1	5	5	5	2
81	7	8	3	1	4	6	4	4
82	6	7	3	0	8	9	7	3
83	15	6	1	1	3	4	6	4
84	16	16	5	2	7	6	8	2
85	15	6	3	2	3	5	7	6
86	8	4	2	0	7	9	2	4
87	6	6	1	2	8	9	11	8
88	3	2	1	0	7	4	3	5
89	14	2	1	0	8	8	10	4
90	16	11	7	1	15	8	10	5
91	11	3	1	1	8	5	8	9
92	8	3	5	0	6	7	9	6
93	9	5	4	1	11	5	9	4
94	4	1	3	0	9	8	5	3
95	10	3	4	0	9	6	9	3
96	7	2	2	2	3	3	5	5
97	6	3	2	0	12	4	6	2
98	2	1	4	1	12	4	2	1
99	6	1	1	0	6	3	3	3
100	11	6	0	0	7	3	4	2
101	3	1	1	0	2	2	4	2
102	4	2	3	0	6	3	4	3
103	4	2	0	0	5	2	2	0
104	8	3	1	0	3	4	5	2
105	4	3	0	1	1	1	4	0
106	5	6	0	0	5	2	1	1
107	4	4	0	0	4	7	1	4
108	2	4	0	0	2	4	3	0
109	6	2	0	0	1	3	1	2
110	8	8	2	0	4	4	4	5
111	7	6	1	0	4	4	3	0
112	8	6	2	3	3	3	5	2
113	8	4	5	0	5	3	4	3
114	8	3	3	1	1	5	3	2
115	5	2	2	0	1	0	0	0
116	10	3	3	2	0	5	2	1
117	8	3	1	0	5	3	5	3
118	9	4	2	0	8	4	0	2
119	4	1	2	1	2	0	0	0
120	10	3	4	1	3	3	2	1
121	4	2	0	1	6	2	1	3
122	7	0	1	1	4	3	4	1
123	8	0	2	0	6	4	4	2
124	9	0	0	0	3	3	3	1
125	3	2	0	0	2	0	0	0
126	9	3	2	2	5	2	4	2
127	5	2	2	1	2	2	1	0
128	6	0	0	0	4	0	4	1
129	0	1	1	0	4	0	1	0
130	7	0	0	0	3	0	2	0
131	3	1	0	0	4	0	0	1
132	3	0	0	0	5	1	6	0
133	4	1	1	0	3		0	2
134	0		0	0	1		0	0
135	2		1	0	0		0	0
136	0		1	0	0		1	1
137	2		1	0	0		0	0
138+	19		3	1	18		10	
Total	463	231	113	40	320	223	242	146

* Special day of non-selective fishing

The size composition of catches taken from various reefs during September 1973 (Table 5) show that males grow to a larger size than females. In both sexes, the size composition tended to be bimodal for each reef, indicating that at least two age groups were being fished. In each sex, each modal size tended to be higher for rock lobsters from Wapa Reef than from Dungeness Reef, probably reflecting better growth rate on Wapa Reef. There was no evidence to support a hypothesis that heavier fishing on one reef had reduced the proportion of larger (older) individuals.

Deeper holes (6-10 m) towards the eastern side of some reefs appear to hold some large rock lobsters but are less accessible because of exposure to prevailing winds and tidal currents.

On the last day of fishing (September 18), the fishermen were instructed to take every rock lobster regardless of size (some selectivity is generally applied as the processors do not want tails of less than 4 oz). However, despite some attempt to locate small rock lobsters, the size composition of the catch on that day (Table 5) was virtually the same as than previously taken on the same reef. The few small individuals seen were too small for the spears being used. The paucity of very small rock lobsters could indicate widely fluctuating year classes or that young juveniles occupy a different habitat. Pyne (1970) observed that in Papua, small juveniles of *P. ornatus* usually occupy very turbid inshore waters of less than one metre depth. Two fishermen reported that they have seen groups of post-larvae in shallow water on Torres Strait reefs in January and February.

None of the female rock lobsters examined during September 1973 carried eggs or sperm masses and the ovaries were pale and undeveloped. Fishermen report that egg bearing *P. ornatus* are very rarely seen on reefs in Torres Strait. Frozen tails of female rock lobsters examined by the author at Thursday Island in June had setose endopodites on the pleopods but as whole specimens were not available, it could not be determined whether these setae carried the previous crop of eggs or were in preparation for the next spawning.

One fisherman reported that in August and September, the larger females taken on the shallow reefs have large orange coloured ovaries but that these rock lobsters disappear in October and November at the same time that adults move out to deeper water seasonally for breeding. Seasonal breeding would be consistent with the observation of a fresh crop of post-larvae appearing at the beginning of each year.

CONCLUSIONS

The very limited data available on the rock lobster resources of Torres Strait do not indicate that the larger reefs which have been fished commercially for several years are overfished. However, fishing intensity is already quite high. Recent catches of over 800 lb (live weight) per day by some vessels are quite comparable with vessels operating in the western rock lobster fishery. There is no management plan for the Torres Strait fishery and insufficient is known of the resource to suggest a sustainable yield. But the fishery is of sufficient local importance to warrant interim management measures while carrying out further studies.

The greatest immediate problem for those operating fishing vessels is to find sufficient local men willing and skilled at diving for rock lobsters. This deficiency acts as the only limitation at present on the overall effective fishing effort, preventing over-exploitation of the resource. This situation could change if more boats and fishermen move in from the south and west (as has begun to occur during 1973).

RECOMMENDATIONS

1. Interim management measures

(a) That vessels fishing for rock lobsters be licensed as such (excepting dinghies at or under 14 ft length). These vessels to be owned and operated only by those who have been resident in Torres Strait for at least two years (or even five years).

(b) That there be no further increase in the number of rock lobster fishing vessels, pending an appraisal of the rock lobster resources of Torres Strait.

(c) That the skipper of each rock lobster fishing vessel be required to supply details of catch and fishing effort for each trip. These data are necessary to assess the condition of the stock. Some skippers already record most of these data.

(d) That deliberate destruction of reef habitat by any means (e.g. crowbars, explosives, etc.) be prohibited.

(e) That poisoning by derris root, or any other plant derivative, or the use of any toxic chemicals, be prohibited.

(f) That the period from November 1 to February 28 be closed to rock lobster fishing (failing this, the closed period should be December 1 to February 28).

(g) That the minimum tail weight of 4 oz presently used by Thursday Island processors, be applied throughout this fishery, pending a review of the resource.

(h) That rock lobster heads should not be discarded on or adjacent to reefs.

The first five of these measures are considered to be most essential. The closed season would prevent any disturbance of the very young rock lobsters present on shallow reefs in December, January and

February. As well as aiding the recovery of the stock after each fishing season, it would also give fishermen a clear period in which to plan for maintenance and refitting. At present, they tend to persist in fishing while they see their colleagues pressing on.

At present there is no indication that the practice of "heading" rock lobsters on the reefs has had an effect upon the distribution of the stock in Torres Strait. As fishermen suggest, predators and scavengers may quickly remove the rock lobster heads. However, both *Jasus lalandii* in South Africa and *Panulirus longipes cygnus* in Western Australia have been shown to be repelled by the dead bodies of their species, and the practice of heading on the fishing grounds has been banned in South Africa. Similar action is advisable in Torres Strait pending further study of the behaviour of *P. ornatus*.

2. Applied research recommended at once

(a) Examination of catch per unit effort data being collected from the fishery, to check for possible trends or differences (1) with time during a year, (2) from one reef to another, (3) in long-term trends resulting from fishing.

(b) Investigation of effects of varying environmental conditions on catch per unit effort. The most important environmental factor in this case may be turbidity, possibly affecting both (1) and (2) above. It will be necessary to measure turbidity regularly at selected site(s).

(c) Examine the composition of catches (especially in length frequency distribution) from one reef regularly throughout a year. Appearance and disappearance of particular modal size groups may indicate immigration or emigraiton of particular age groups, while a shift in a mode will give an indication of growth rate.

(d) Apply a high level of fishing pressure on one reef and maintain through successive months, checking for a decline in catch per unit effort by a known fishing effort. Charter of a fishing vessel and team would be required (possibly in close association with other fishing vessel(s) in the initial stages). It is important that the fishing effort be documented in detail. Check for subsequent recovery in following year(s).

(e) Investigate alternative methods for capturing *P. ornatus* alive. This is necessary for the fishery if aiming to meet export requirements. It is also needed as a pre-requisite for certain biological studies (measurement of population density, growth rate, migration, etc.). Tangle nets (set along the path of the tidal current) or shelters (used with some success on *P. argus* in Cuba) might warrant trials.

(f) If live capture has been resolved, tag a significant proportion of a population on selected reef in order to (1) measure population density by mark-recapture, at a period when little migration is occurring,

(2) measure growth rate (important to know whether recruitment into the fishery is at 2 yr or 5 yr of age). (3) follow migration.

(g) Trawl deeper waters in Torres Strait (charter vessel) at selected times and places to resolve annual migration (linked with tagging (f) (3) above).

(h) Maintain collectors (Phillips 1972) for puerulus larvae at selected site(s), checking monthly for the relative strength of larval settlement. This will give an index of variability of year class strength which may be expected.

(i) Check experimentally whether dead bodies repulse living *P. ornatus*.

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DISCUSSION

A population approaching an equilibrium with its environment becomes limited by one (or more) of the environmental pressures restricting further growth. For example, as a population approaches the limits of accessible food resources there may be a diminution of individual growth rates, a delay in age at first breeding, a lowered fecundity, and increased mortality especially of the young. In such a population the recruitment coefficient (r) declines and the natural mortality coefficient (M) may increase, until $r = M$ and the population is at its maximum for the environmental pressures operating at that time.

If the environmental pressures did not fluctuate greatly over a long time-span, or if members of a species are so long-lived that the impacts of short-term fluctuations in environmental pressures are dampened, a population would remain close to its maximum size for a considerable period. In such a population it would be possible to assign constants for growth rate, age at first breeding, fecundity, infant and adult mortality. Indeed, having measured one or other of these variables, some research workers have tended to refer to them as constants for that species rather than as the resultants for a population exposed to a specific set of environmental pressures.

The values of population parameters when $r = M$ are less important than the capacity of that population to respond when the limitations of environmental pressures are relaxed. In other words the extent to which growth rate, age at first breeding, fecundity, infant and adult mortality change when environmental pressures are alleviated determines the maximal value of $r - M$. For those species exploited commercially, the flexibility of these population parameters determines the level of the maximum sustainable yield.

Food supply is a factor which is likely to have limited population size in humpback whales. Before whaling commenced populations were probably at steady maxima. Then humpback whales gathering to feed on the dense concentrations of euphausiids present in Antarctic surface waters during the southern summer would have been exposed not only to intraspecific competition but also to interspecific competition from other species of baleen whales, seals, birds, etc. Possibly the competition from other species of baleen whales might have been less direct because of differences in growth stages of euphausiids preferred and hence in location where a species congregates (eg., blue whales feeding in higher latitudes than humpback whales). Nevertheless, competition for food may have been such that an individual humpback whale could no longer filter sufficient water to obtain the 1 to 1.5 tonnes estimated as required per day. Growth may then have been depressed and maturity delayed. Under such conditions some humpback whales might have stayed longer in Antarctic waters in search of food, some perhaps remaining there throughout the winter. Reduction of the period spent in temperate and subtropical waters during the winter (breeding season), or a decrease in the proportion of the population making this migration, might have reduced the conception rate. There may also have been a decline in maternal care by females obliged to search more actively for food, resulting in earlier weaning of calves and increased mortality of young.

Humpback whale populations approaching maximum levels may be also limited through behavioural stresses imposed upon the social structure of the population. The importance of this aspect on mammalian populations has been reviewed by Myers (1966). Such stresses upon social psychology within humpback whale populations are more likely to occur on the breeding grounds rather than on the feeding grounds. During the breeding season, humpback whales are concentrated in coastal waters of temperate and sub-tropical regions so that towards the upper limit of population size, density would then be high. This species does not appear to have a highly developed social structure, generally remaining in quite small groups of two or three individuals, groups of ten or more seldom being recorded (at the moderate to low levels of populations examined). It is not known whether a male and female remain together for more than a few days or weeks during the breeding season. Competition between males does not appear to be very intense, though some of the behaviour generally regarded as "play" in this species might in fact be male display intended to achieve dominance.

At the moderate level of the Group IV population present on the west coast of Australia in 1952 (Paper 5), the author noted on several occasions that a group of humpback whales appeared to consist of one oestrous female and several mature males. As the population was reduced in succeeding years, such groups were rarely seen. It is suggested that as a population of humpback whales approaches its peak, this grouping of several males to each oestrous female may be of more frequent occurrence. Within such a group, male display and interference while not particularly aggressive, might preclude successful mating. In the case of female humpback whales having a post-partum ovulation, the presence of several bulls could also affect maternal behaviour so that the young calf was more exposed to predators.

At high population levels, competitive activity of bulls moving from one oestrous female to another could lower the reproductive rate (and possibly cause some increased mortality of calves). As indicated in Paper 14, only a slight fall in the recruitment coefficient (r) would bring this into balance with the natural mortality coefficient (M), halting any further increase in population size.

Another means by which population growth may be limited is by increased incidence of parasites and disease at high levels of population density. This has been demonstrated to play a role in the Alaska fur seal (Kenyon, Scheffer and Chapman, 1954) where increased mortality of pups (mainly due to hookworm) occurred at high population density. There is no evidence of such factors operating to limit population growth in humpback whales. Similarly there is no indication that predation plays an important role in limiting humpback whales. As in the fur seals (Chapman 1961), any increase in predator population would have greatest impact on the young.

In humpback whales loss of calf soon after parturition (when the young are most vulnerable) results in an immediate renewal of oestrous cycles (Paper 4) so that this species can compensate to some extent for early loss of calf.

If undisturbed populations of humpback whales are held at a maximum by the combined effects of limited food supply and behavioural stresses as suggested above, the removal of these limitations by means of commercial exploitation reducing population size could be expected to result in increased growth rate of survivors, earlier age at maturity, an improvement in birth rate, and some decrease in mortality of the young.

Examination of the data from the two populations of humpback whales reported here shows that during exploitation there were transient increases in recorded lengths of females reaching puberty (Paper 12), and similar temporary increases in the recorded lengths of young humpback whales aged three to eight years (Paper 14). These changes did not result from increased growth but were artefacts resulting from selectivity applied by whalers as quotas were reduced. No change in the age at puberty was observed (Paper 9). The percentage of adult females which were pregnant varied considerably from year to year (Paper 11), but no evidence was found of a change in birth rate as a result of exploitation of either population. The method employed to separate the total mortality coefficient (Z) into fishing mortality (F) and natural mortality (M) (Paper 14), assumed that natural mortality of adults did not vary significantly over the study period. Subsequent examination of the state of these populations gave some support to this assumption.

The question must then be asked whether the above findings negate the original hypothesis (ie., that when exploitation commences upon a population at its maximum, compensatory changes occur in growth rate, reproductive rate and survival). An explanation is found when with the advantage of hind-sight, the condition of both populations of humpback whales at the commencement of the study are re-assessed.

The maximum level of the Group IV population when undisturbed was towards 17,000 whales (Paper 14). When hunting re-commenced in 1949 the stock was still recovering from the intensive hunting from 1934 to 1938. The population had risen to approximately 10,000 individuals, the level at which it is suggested that r - M is maximal. At that point then, growth rate, birth rate and survival would have been optimal. The maximum sustainable catch from this population was estimated to be 390 whales per year. However, from 1950 the annual catch from the Group IV population ranged from three to six times the maximum sustainable yield. Stock size then declined rapidly with no prospects for compensatory changes in recruitment or natural mortality. The stock-recruitment relationship was linear (Paper 14, Fig. 33), representing only the descending left-hand limb of the expected asymptotic curve.

A similar situation applied in the Group V population of humpback whales. In the unfished state the maximum size of the population was some 10,000 whales so that the maximum sustainable yield would have been less than that of the Group IV population if similar values for recruitment and natural mortality applied. In 1948 the Group V population was probably close to its maximum but by 1950-51 was reduced to approximately 8,500 whales, the level of the maximum sustainable yield (330 whales). Throughout the next ten years the annual catch was well in excess of the maximum sustainable yield (Paper 14, p.40). Biological data collected during this period would not show any trend toward increasing growth rate, earlier age at maturity or improvement in birth rate.

Another factor here is that earlier depletion of southern blue and fin whale populations could have reduced interspecific competition by humpback whales for food, so that this limiting factor may have been lifted even before intensive fishing of humpback whales began about 1950.

In the absence of evidence of compensatory changes in population processes as these humpback whale populations were exploited, the original hypothesis might be questioned in the case of whale populations. It has seldom been possible to obtain data upon population processes of whale populations which are at a maximum. Laws (1977 a,b) has recently reviewed the data from the once large populations of southern blue and fin whales, presenting evidence that the growth rates and pregnancy rates increased and mean ages at sexual maturity decreased during the early phase of expanding whaling operations, in response to increased food availability. In the case of sei whales similar increases in pregnancy rates and earlier maturity preceded heavy exploitation of the species, apparently resulting from an alleviation of competition for food as the larger species of baleen whales were exploited first.

The western rock lobster population presented far better opportunities to test the hypothesis set out earlier. Despite the fact that relatively heavy exploitation had been in progress for some years before the present research was begun (Paper 15), the very restricted dispersion and mixing (Paper 20) of the population (except during the larval phase; Paper 16) has allowed segments of the juvenile and adult population to respond independently to localised differences in both environmental and fishing pressures. In addition, the successful use of the western rock lobster as an experimental animal reared from the puerulus larval phase in aquaria under controlled environmental conditions (Paper 19, 21, 22) has assisted greatly in the interpretation of processes occurring within the natural population.

Growth rates of juvenile western rock lobsters varied from one locality to another, being lowest in the area where density was highest (Paper 24). From controlled experiments in aquaria (Paper 22) and experimental reduction of competition on a crowded nursery reef (unpublished data), food supply has emerged as the dominant factor determining growth in the natural population in spite of the wide diversity of species eaten (Paper 22). At a locality where the density of adults is still high, adults are generally stunted while in other areas where fishing has reduced the density of adult stock very considerably, the size composition of adults is much higher (Paper 25).

Across the population as it stands presently, the mean size of females at first breeding varies greatly being smallest at the locality where adult density is greatest, and largest in the area exposed to the longest period of exploitation (Paper 25). In the latter area there is some evidence that the mean size at first breeding was less in the earlier phase of exploitation over 20 years ago.

The age of females at first breeding is difficult to assess in the wild population but has been estimated to be at seven to eight years of age where there is restriction of growth rate of juveniles (Paper 25). However, under more optimal conditions in aquaria, one group of females commenced breeding at ages ranging from 4.9 to 5.7 years (Paper 19), while in a recent experiment under more uniformly optimal conditions breeding commenced as early as 3.0 years of age (unpublished data). Thus there is a considerable degree of flexibility in age at first breeding in this species.

Because there is a direct relation between size of female and number of eggs in a single spawning, fecundity is inversely related to population density through changes in growth rate (Paper 25). In addition, the frequency of spawning increases with improved food supply (Paper 25). Both factors operate to increase the density dependence of fecundity in this population.

On the nursery reefs a direct relation has been shown between natural mortality and density of juveniles (Papers 17, 23). Food and shelter are suggested to be the limiting factors here. Earlier results in aquaria indicated that crowding caused behavioural stress (greater aggression) resulting in increased mortality despite the presence of surplus food (Paper 17). However, subsequent experiments (Paper 22) showed that food had been limiting in the original experiment, and that when food was clearly in excess, crowding did not result in higher natural mortality.

An interesting facet of the experiment demonstrating increased mortality under limited availability of food was that this selected against aggressiveness and high growth rate. Those rock lobsters which were larger and/or more aggressive succeeded in obtaining a higher proportion of the available food. This enabled them to moult earlier than those competing less successfully for the food. However, immediately after ecdysis the soft shelled animals having very little defense were then killed and eaten by the unmoulted, more poorly fed individuals. This selective pressure decreased as food became abundant.

The processes outlined above have interacted within the western rock lobster population as it has been exposed to high (but controlled) fishing pressure (Paper 26). When population density has been reduced, the sizes of females at first and subsequent spawning have increased, and the age at first breeding reduced. These responses, together with an increase in frequency of spawning, resulted in high fecundity amongst the reduced numbers of breeding females remaining. This has had no impact upon subsequent recruitment to the fishable stock while settlement of larvae upon nursery reefs has been in excess of the carrying capacity of those shallow reefs. Because growth and survival of juveniles are density dependent during the 4-5 years spent on nursery reefs, this is a major buffer against fishing pressure.

In conclusion then, populations of whales and rock lobsters have similar basic responses when exposed to exploitation, with compensatory changes in processes leading toward increasing recruitment. However, the capacity to respond contrasts sharply: In the humpback whale it is extremely low so that the maximum sustainable catch is only a few hundred individuals per year, whereas in the western rock lobster the much higher flexibility enables a sustainable catch of several millions per year.

By coincidence, when these sustainable catches are converted to sustainable yields in terms of weight, they are of similar magnitude (8,000 to 12,000 tonnes per year).

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