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THE ECOLOGY OF LEPSIELLA VINOSA (MOLLUSCA; GASTROPODA)

WITH PARTICULAR REGARD TO ITS FEEDING BEHAVIOUR

by

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30	line	5	for	Connell (1961)	read	Connell (1961a)
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34	line	3	for	Connell (1961)	read	Connell (1961b)
66	line	13	for	Landenberger (1967)	read	Landenberger (1968)
72	line	3	for	<u>Helix pomatia</u>	read	<u>Helix pomatia</u>
74	line	11	for	Connell (1961)	read	Connell (1961a)
112	line	26	for	P = 0.24	read	P = 0.78
112	line	28	for	P = 0.255	read	P = 0.74
114	line	18	for	P = 0.085	read	P = 0.10
115	line	27	for	P = 0.39	read	P = 0.71
118	line	7	for	P = 0.33	read	P = 0.56
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SUMMARY

Lepsiella vinosa is a muricid gastropod which is found in South Australian mangroves where it eats two species of barnacles, Balanus amphitrite and Elminius modestus, which are attached to the pneumatophores and branches of the mangrove Avicennia marina.

The distribution of pneumatophores is heterogeneous and distinct prey patches are formed. A series of these patches were surveyed to determine the impact of L. vinosa predation on the barnacle populations and the influence of barnacle density on prey selection by the predator.

B. amphitrite settles between Spring and mid-summer. It is subject to fluctuations in reproductive success and "failures" were recorded in 1975 and 1976. L. vinosa eliminated 9.3% to 30.8% of the heavy 1974 Spring settlement in one year. After three years only those B. amphitrite which settled in refuges survived. L. vinosa could potentially eliminate all B. amphitrite in the patches between successive breeding seasons.

E. modestus can settle continuously and unlike B. amphitrite its numbers recover quickly after a "catastrophe". In crowded situations it is crushed by B. amphitrite. Frequent restocking of the patches prevent its elimination by L. vinosa predation.

Prey selection by L. vinosa is influenced by both relative and absolute densities of the barnacle species. At moderate densities less than 25 barnacles/metre pneumatophore, the predator fed proportionally; L. vinosa feeding on the less abundant species changed to the more abundant species as its relative density increased. At high densities, 50 to 70 barnacles/metre pneumatophore, E. modestus was progressively dropped from the diet as the absolute density increased.

Laboratory experiments indicate that L. vinosa can be trained to either barnacle species and shows switching in terms of Murdoch's (1969) model. Field cage experiments indicate that L. vinosa shows switching provided that the absolute density of B. amphitrite is not too high. The switch tends to become stronger over an eight week period.

In both the laboratory and field experiments L. vinosa had a weak preference for B. amphitrite, $c = 1.26$, when equal numbers of each species were present. The preference appears to be consistent between individual L. vinosa.

In the field L. vinosa switches to B. amphitrite when it is more abundant irrespective of prior training. L. vinosa trained to E. modestus or unfed switched to E. modestus when it was more abundant. Those trained to B. amphitrite however only slowly switched to E. modestus over a period of eight weeks. A clumped prey distribution accelerated the switch.

L. vinosa also showed asymmetry in feeding rate. Those trained to E. modestus fed at the average rate irrespective of the prey presented. L. vinosa trained to B. amphitrite showed a marked reduction in their feeding rate when B. amphitrite was less abundant.

The functional response to both species appears to be type 3 and is therefore potentially stabilising. Different mechanisms are however responsible for the rapid acceleration in the number of a prey species consumed. The low consumption of E. modestus when it is rare is due to L. vinosa concentrating its attacks on B. amphitrite. Switching to E. modestus as it becomes relatively more abundant causes the rapid acceleration in the number of E. modestus consumed. The low consumption of B. amphitrite when it is rare is due to a low overall feeding rate. An increase in

B. amphitrite density increases both the feeding rate and proportion of B. amphitrite in the diet causing a rapid acceleration in the number of B. amphitrite consumed.

L. vinosa thus shows a potentially stabilising functional response which is more complex than a simple change in prey preference with relative prey density.

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DECLARATION

This thesis contains no material previously submitted by me for a degree in any University. To the best of my knowledge it contains no material written or published by another person except where due acknowledgement is given.

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1.1 Introduction

This thesis examines the interaction between the gastropod Lepsiella vinosa (Lamarck, 1822) and the barnacles Balanus amphitrite (Darwin, 1854) and Elminius modestus (Darwin, 1854) in South Australian mangroves. The primary aim was to determine if L. vinosa shows switching in response to changes in the densities of the barnacle species in the field. Murdoch and Oaten (1975) have emphasised that although mathematical models and laboratory studies on the subject of predator switching and population stability are well developed there is a lack of field studies.

Switching is potentially important and is an attractive concept as it could provide a comparatively quick mechanism for stabilising prey populations (Murdoch 1969). However a field study is necessary as laboratory studies can only determine if switching is possible as a behavioural response under artificial conditions. The feeding behaviour of a predator would only affect the stability of its prey species if predation were sufficiently heavy to influence prey density in the field. In a co-evolved predator-prey interaction this may not be the case and other factors may be more important.

A predator-prey interaction in the marine intertidal zone is likely to be suitable for a field study of switching. There is considerable evidence to suggest that many invertebrate predators have a marked influence on the structure of marine intertidal communities (Paine 1966, Connell, 1970, Lubchenco and Menge 1978). Furthermore Murdoch (1969) has demonstrated that a predatory gastropod, Acanthina spirata, shows switching under laboratory conditions.

Some aspects of the interaction between L. vinosa and its barnacle prey species are especially favourable for a study of switching. It is essentially a one-predator-two-prey species interaction as L. vinosa infrequently attacks other species. Co-adaptation between the predator and the two prey species could be expected with some form of behavioural

adaptation by the predator with regard to foraging.

The prey are sessile and the predator takes several days to consume a barnacle. As a result estimates of prey density and the predator's prey selection can be made more accurately than is usually expected in a field study. In addition field cage experiments in which prey densities can be manipulated are possible.

The major problem in using the L. vinosa-barnacle interaction to study switching arises from the predator's slow feeding rate. Experiments take a long time if a reasonable sample size is to be obtained.

The approach used in this study was firstly to investigate the predator's feeding behaviour in naturally occurring prey patches and then to use controlled experiments to concentrate on the switching response. It was not possible to examine aspects other than switching in detail. Nevertheless surveys of the predator's feeding behaviour in the field and also the settlement patterns of the prey species give an indication of the importance of switching in the interaction.

A brief description of the location of the study and general features of the intertidal zone at Port Adelaide are given in Chapter 2. The results obtained from surveys of naturally occurring prey patches are presented in Chapter 3 to 7. A total of eight patches were surveyed at intervals of two to four weeks over a period of almost a year.

In Chapter 3 the settlement patterns, competitive interactions and seasonal reproductive success of the prey species are presented. These factors are important as they indicate aspects of the biology of the prey species to which the predator has adapted.

Some aspects of the feeding behaviour of L. vinosa are presented in Chapter 4. The influence of prey density and season on the feeding rate of L. vinosa in the field are quantified. Laboratory experiments on the growth rate of L. vinosa on pure diets of each prey species are reported. The predator's prey evaluation procedure is described.



Plate 1. L. vinosa on a pneumatophore between two barnacles.
The barnacle at the top of the pneumatophore is E. modestus
and the barnacle below L. vinosa is E. amphitrite.
(Magnification x 1.75)

The dynamics of the barnacle populations in a series of prey patches in the field are described in Chapter 5. The influence of L. vinosa predation on the barnacle species is quantified and compared with other factors causing barnacle mortality.

The movement of L. vinosa in prey patches is examined in Chapter 6. Migration patterns and the duration individual L. vinosa remain in a patch are described.

Prey selection in the field is examined in Chapter 7. The influence of changes in the relative and absolute densities of the prey species on the predator's diet are reported.

Chapter 8 and Chapter 9 are concerned with the switching behaviour of L. vinosa. In Chapter 8 preliminary laboratory experiments which examine the suitability of using the L. vinosa-barnacle interaction to examine switching are reported.

In Chapter 9 switching is examined in field cage experiments. Artificial pneumatophore patches in which the density of the prey species were controlled were established in field cages. The experiments examine the predator's prey choice and feeding rate at different prey ratios.

A brief review of factors influencing the stability of the L. vinosa-barnacle interaction is given in Chapter 10.

1.2 Literature

Population ecology is concerned with the abundance of animals and predation is one factor which is important. In this brief literature review only one aspect of predation is considered, the predator's functional response.

Authors of papers in this field refer to their studies under usually one of the following headings; switching, searching image, apostacy or in relation to Holling's categories of functional response. It is therefore natural to group these studies under these headings although most of the studies could be placed under more than one of the headings.

Switching is considered first as this thesis is mainly concerned with this concept. Most papers considered under the other headings are equally relevant to switching as this concept implies a numerical result and is not concerned with mechanisms.

Ornithologists have been particularly interested in the searching image concept and the volume of literature on this subject is greater than for the other headings. Some papers are concerned with the mechanism itself, but many of the papers can be examined for evidence of switching in birds.

1.2.1 Switching

Murdoch (1969) offers the following definition of "switching".

"As a prey species becomes relatively more abundant, switching occurs if the relative amount which that species forms of the predators diet increases disproportionately in comparison with the expected amount." Switching implies a numerical result rather than a mechanism (Murdoch and Marks 1973).

"The null case of no switching is written $\frac{P_1}{P_2} = C \frac{N_1}{N_2}$, where $\frac{P_1}{P_2}$ is the ratio of the two species in the diet, $\frac{N_1}{N_2}$ is the ratio available in the environment and C is a constant" (Murdoch and Marks 1973). The constant "C" is an "operational measure of preference and can be defined as the ratio of prey 1 to prey 2 in the diet when two prey species are equally abundant" (Murdoch and Marks 1973).

In this thesis I will only use the term "switching" in the sense of Murdoch's (1969) definition. The term "switching" has also been used to describe a change from one prey type to another which is not necessarily frequency-dependent. Curio (1976) has reviewed papers which use the term in this sense.

1.2.2 Experimental studies

Murdoch and Oaten (1975) have extensively reviewed the literature on studies which provide evidence for and against switching.

In some cases they re-examined unpublished data provided by authors whose papers were not directly related to switching. I will therefore only review the major features of these studies and indicate the conclusions which are relevant to switching.

Predators which have shown switching for some prey combinations in laboratory experiments are Acanthina (Murdoch 1969), guppies (Murdoch et al. 1975), rudd (Popham 1941), Stentor (Rapport reported in Murdoch and Oaten 1975) and Notonecta and Ischnura (Lawton et al. 1974). Murdoch and Oaten (1975) conclude that switching is unrelated to the predator's phylogenetic position as it has been found from protozoa to birds. In some cases, Stentor and Acanthina, the same predator would show either switching or non-switching depending upon the prey species involved (Murdoch et al. 1975).

Different mechanisms are proposed to explain the switching response. Acanthina required prior training to produce switching between its barnacle and mussel prey. The mechanism involved is suggested to be variable rejection rates. The predator moves over the prey at random handling many individuals before attacking a particular individual. The selective value could be either that it is more efficient physiologically to concentrate on one prey species or possibly that it is more efficient to use only one type of attack method (Murdoch et al. 1975).

Guppies however require no prior training and do not reject any prey they encounter. The mechanism which produces switching is their response to absolute reward rates in alternative sub-habitats. The prey were Drosophila, found on the waters surface, and tubificid worms which were on the bottom. The guppies sampled and distinguished between the reward rates in the two sub-habitats. Feeding in the better sub-habitat produces switching as the more abundant prey would be represented disproportionately in the diet. The selective advantage is that a switching predator would encounter prey more frequently if it sampled while the cost of sampling

is small.

Notonecta showed switching for Asellus and mayflies as alternative prey. Lawton et al. (1974) suggest that the basis for switching is that the proportion of successful attacks increases as the abundance of prey increases. The encounter rate remains the same as there is no evidence of search image formation and selection is not in "runs".

Ischnura appears to be a further example of a switching invertebrate predator. The basis of the switch is not known.

Quail (Manly et al. 1972) and pigeons (Murton 1971) also produced results consistent with switching in the field. The mechanism could be due to relative "discovery" rates in which the rarer species has less chance of being seen. A search image could be involved.

Murdoch (1969) suggested that predators which switch should have weak but variable preferences among individuals at equality, that is when equal numbers of prey are available. All the above listed predators satisfy this generalisation with the possible exception of Notonecta which developed similar diets as the experiments progressed. Murdoch et al. (1975) suggest that the Notonecta experiment indicates that the generalisation may not apply if attack success rather than preference varied.

Predators which have a strong and consistent preference do not switch (Murdoch 1969). Two examples illustrate this generalisation, Thais (Murdoch 1969) and Stentor feeding on Tetrahymena and Euglena.

If the C value is greater than 3 preference is strong (Murdoch et al. 1975). Thais feeding on the mussels Mytilus californianus and Mytilus edulis had a C value of 10. They could not be trained to the less preferred species and did not switch. Stentor had a C value of 3 to 6 for Tetrahymena over Euglena and consistent diets (Murdoch and Oaten 1975 analysis of Rapport's data).

Two predators which have weak and consistent preferences at equality have been found not to switch. These are ladybirds feeding on two aphids (Murdoch and Marks 1973) and the bluegill sunfish feeding on mosquito and midge larvae (Reed 1969 reported in Murdoch and Oaten 1975).

Ladybirds cannot be trained to either prey and eat any prey they encounter. Prey are found by bumping into them. Similar results have been found for the mite Zetzellia mali (Santos 1976).

1.2.3 Switching and Stability

The predator-prey interaction examined in this thesis is stable in the sense that it continues to persist. In mathematical models a system is considered stable if the system returns to an equilibrium point after a small perturbation (Lewontin 1969, May 1973). The assumption that these two concepts of stability are related is the basis for suggesting that features which are found to be important in a mathematical model could also be important in a field situation (Murdoch and Oaten 1975).

Switching refers only to relative number of attacks and to relative prey abundance. The mortality on either prey species is not necessarily density-dependent but only frequency-dependent (Murdoch and Oaten 1975). If the functional response to the prey density is type 2 (Holling 1959b) then there is no contribution to the stability of a predator-prey interaction (Hassell and May 1973, Oaten and Murdoch 1975a).

Switching has the potential to produce stability (Murdoch and Marks 1973). Nevertheless it is possible to have switching and yet not have a stabilising functional response. Unfortunately there is little experimental evidence concerning the relationship between switching and functional response to each prey species (Oaten and Murdoch 1975b).

Murdoch (1977) has argued that although a stabilising functional response may contribute to the stability of a prey species it is neither necessary nor sufficient for its stability. The stability of a prey species will have some influence on the stability of the total community, but it

is not likely to be either a sufficient or necessary condition for community stability. Levin (1977) has argued that a number of mechanisms can compensate for a destabilising functional response and produce stability in a system.

Steele (1974) produced a computer model in which switching failed to produce stability. If each individual predator-prey system is unstable switching can result in overall instability.

A number of models have been produced to examine the effect of switching on a competing prey species. Switching can make possible a significantly greater degree of niche overlap among competing prey species (Roughgarden and Feldman 1976). Comins and Hassell (1977) state that even a moderate amount of switching enlarges the domain of parameter space in which the two prey species can co-exist. It is advantageous to the predator as it allows it to co-exist with its prey over a wider range of conditions. May (1977) suggests that switching can make it easier for prey species to co-exist, and could therefore lead to more diversified communities at the species level.

1.2.4.1 Searching Image

The concept of searching image was introduced by von Uexkull (1934) in connection with what he described as puzzling actions by people and animals which occur without the relevant sensory stimuli. He suggested that repeated personal experiences can lead to the formation of a search image which annihilates the perceptual image. Animals are hypothesised to live in what he describes as an "unwelt" or magic world of subjective realities. He based his ideas on personal experiences, observations of children and animals and did not specifically emphasise its role in predation.

Tinbergen (1960) applied the concept of searching image to predation by birds, principally the great Tit Parus major, in Dutch pine forests. He attempted, as a part of an extensive field study of bird predation on insects, to determine the relationship between the density of a prey species and the percentage it formed in the birds diet. He suggested that, after risk indices were taken into account, the relation between

the density of a prey species and its percentage in the food cannot be explained from probability of encounters alone. At low density a prey was consumed less than would be expected. At moderate density it suffered unexpectedly high predation which again falls below expectation at high density.

To explain the change in consumption between low and moderate densities he postulated that the birds adopt a specific searching image once a species became sufficiently common. The predator "learns to see" the prey due to a "sieving operation of the visual stimuli reaching the retina." This causes the birds to concentrate their attacks on this species. The decrease in consumption below what is expected at high densities is suggested to be due to the birds ceasing to use the searching image when a prey species forms more than a certain critical percentage in the total food. This enables the birds to vary their diet.

Tinbergen (1960) suggested that the advantage for the birds in forming searching images is that it increases their efficiency in locating prey. The prey are often cryptic and usually occur at low density mixed in a tremendous amount of needles and twigs. Support for this argument can be found in the experiments of de Ruiter (1952) who demonstrated that jays and chaffinches take a long time to find sticklike caterpillars placed among twigs. Once the first caterpillar was found the birds subsequently picked out the other insects without pecking at any of the twigs. Similar delays before a prey is detected have been reported for captive tits seeking cryptic moths (Kettlewell 1955), caged thrushes seeking the snail Cepaea nemoralis (Clarke 1962), and captive tits seeking green morphs of the larvae of Bupalus piniarius (Den Boer 1971).

There is some difficulty in distinguishing between the formation of a searching image and a "latent phase" during which an unfamiliar prey is rejected. Beukema (1968) found that sticklebacks which were accustomed

to hunting for Tubifex ignored new prey species when they were first introduced. After 50 to 200 encounters the sticklebacks began to eat the new prey and their reactive distance to them increased over the next 60 or more encounters. There are two possible explanations for these results; either the sticklebacks formed a searching image or they required time to become familiar with the new prey.

Ware (1971) found a similar response for rainbow trout using white and black dyed pieces of chicken liver as prey. The Test Tank was painted black so that the black prey were cryptic and the white prey conspicuous. Training consisted of feeding the trout one prey type at 48 hour intervals. The trout initially did not feed on the prey, but once they started their reactive distance increased over several days. This result was obtained for both cryptic and conspicuous prey and indicates that the trout simply built up a preference for familiar prey. The alternative explanation that they formed a searching image can be rejected as the white prey were always easy to see.

Dawkins (1971a) conducted a series of laboratory experiments to test the searching image concept. Chicks were used as predators and the prey consisted of dyed rice grains which were placed on different coloured backgrounds. The results were compatible with the searching image hypothesis as the chicks showed striking improvements in their ability to detect cryptic food which is most plausibly seen as a central change of perception. The change was not retained after 24 hours and feeding conspicuous grains adversely affected their ability to detect cryptic grains. Furthermore Dawkins (1971b) argued that the formation of a searching image involved a switch of attention. Chicks pecking on conspicuous grains attended to colour cues while those looking for cryptic grains did not.

Some support for the searching image concept has been obtained from the results of experiments using human subjects. Neisser (1964, 1967) reports that while searching for relevant items human subjects do not

see meaningless items and that everything is blurred except the sought item which suddenly stands out. Broadbent (1965) suggests that the nervous system is limited in its ability to process sensory data and must operate selectively and economically. To reduce the amount of information which reaches the sensory receptors a selective "filter" which blocks some and passes others to a single decision channel is hypothesised by some authors (Treisman 1964, Engel 1971).

Field experiments to test the searching image hypothesis are extremely difficult to carry out as it is difficult to measure the availability of prey and to observe the predators behaviour in detail (Krebs 1973). The data provided by Tinbergen (1960) and by Mook, Mook and Heikess (1960) provide very poor support for the concept. Murdoch and Oaten (1975) have reviewed the evidence presented in these papers and conclude that on the whole risk is not related to fluctuations in absolute density of the prey.

Croze (1970) attempted to overcome the problems in obtaining field results by making observations of hand raised and wild carrion crows on a beach using artificial prey. The prey consisted of painted mussel shells which were placed over pieces of meat which acted as a reward. The shells appeared to the human eye to be highly cryptic when mixed with beach pebbles. He showed his hand raised crows a shell of one colour which they turned over and found the meat. After two or three demonstrations the crows were able to select the right colour when wandering around the beach looking for prey. The results were interpreted by Croze to indicate that the crows formed a searching image on the basis of two or three experiences.

Field experiments have also been carried out by Murton (1971) using wild pigeons, Columba palumbus, as predators and several types of cryptic grain in clover fields. The seeds were treated with a stupefying drug and the contents of the birds crops were examined after they had drugged themselves. A high percentage of the birds, 72%,

specialised on one type of seed when two seed types were equally available. Murton regards this as evidence of searching image formation.

Gibb (1962, 1966) examined predation by tits on Ernarmonia conicolana which are concealed just beneath the cuticle of ripening pine cones. Predation was found to be exceptionally light at very low densities but increased abruptly with a slight increase in density. He argues that, as the larvae are located by tapping, the birds must have a searching image which is tactile rather than, or as well as, visual. At low densities he suggests the birds avoid forming a searching image as the prey are uneconomical. Furthermore he suggests that the tits were preying by expectation and left the cones after the expected number of larvae were found. Preying by expectation could explain the levelling off in a sigmoid curve at high densities.

Simons and Alcock (1971) however recalculated Gibb's data on the basis of the number of larvae eaten per cone instead of percentage eaten. They questioned whether his results did in fact show that the birds stopped searching after finding a fixed number of larvae. This recalculation is a serious criticism of Gibb's hypothesis.

Another challenge, on the basis of human economic theories, was made by Tullock (1969). He suggests simply that the disproportionate attack on patches of varying larval density could come about by the tits concentrating on patches of highest larval density while others are depleted only slightly. Curio (1976), however, believes that this alternative explanation is unlikely as it involves a pattern of foraging which is not consistent with field observations of the way tits forage.

1.2.4.2 Profitability of hunting

Royama (1970) put forward a new hypothesis, based on the concept of profitability of hunting, to explain the sigmoid functional response curve which Tinbergen claimed for the great tit. He argued that due to the need to constantly maximise hunting efficiency the birds concentrate their

search in areas of high food abundance. If the birds spend their time in a "niche", used here to mean prey patch, in proportion to its profitability and continue to sample other "niches" to test their profitability then a sigmoid curve for predation with increasing density will result. The initial low predation on a new prey is due to the birds regarding it as unprofitable. Acceleration in the predation at moderate densities is due to the birds finding the "niche" and spending most of their time in it. The levelling off at high densities is due to sampling other "niches" and the limitations on increased prey consumption due to handling time.

To support this hypothesis Royama claimed that direct observations indicated that the birds were exploiting feeding patches rather than prey species. He also argued that the same prey species were carried to the nest in "runs" which is compatible with his hypothesis but not Tinbergen's idea of random encounters. This argument can be criticised as in fact random encounters are only a part of Tinbergen's null hypothesis and not necessary to the searching image concept (Curio 1976). Furthermore Dawkins (1971a) found that searching image formation led to such "runs."

Royama does not deny the possibility of searching images existing but argues that Tinbergen's results cannot be explained on the basis of this hypothesis. He extensively criticises Tinbergen's hypothesis as it is based on inappropriate assumptions, involves contradictions of the observed facts and because two different explanations are required to explain deviations from the expected predation rate at low and high densities. The advantages of rejecting a species while the searching image is being formed and the rejection of large but rare prey species are queried.

More technical criticisms include the observation that although there is a delay before the appearance of a new prey species in the diet it also ceases to be preyed upon before it becomes rare. Parents eat different prey ^{from} the young. Some very common and palatable prey

are not taken in large numbers which is inconsistent with searching image formation.

Support for Royama can be found in the experiments of Smith and Dawkins (1971) who showed that great tits in laboratory studies concentrated their search for mealworms in high density areas. Smith, Hugh and Sweatman (1974) examined food seeking behaviour of tits in patchy environments in the laboratory and the field and concluded that their results supported Royama's hypothesis. Even one reward is sufficient to cause tits to search preferentially in one of several potential food sites (Krebs, MacRoberts and Cullen 1972).

Redshanks, Tringa totanus, are also reported to concentrate their searching effort in profitable areas (Goss-Custard 1970). Goss-Custard (1977) further examined Royama's model of predation for redshanks on Corophium in the field. The results in general support the concept of profitability of hunting and there is a slight suggestion of a sigmoid curve being obtained.

Alcock (1973) argues that both Tinbergen's and Royama's hypotheses may be correct. Observations on the red-winged blackbirds, Agelaius phoeniceus, indicated that locational cues associated with the prey are used when foraging. Nevertheless specific visual cues associated with the prey are also probably used by some birds at the same time.

1.2.5 Searching Image formation and the concept of switching

Murdoch and Oaten (1975) have extensively discussed the relationship between the concepts of searching image and switching. They conclude that the two concepts are not equivalent. The fundamental difference is that searching image formation does not refer to changes in the predators' behaviour in response to a change in the relative density of one prey with respect to the other prey (Murdoch and Oaten 1975). It is essentially concerned with the predators' response to an increase in the absolute density of the main prey species. The prey density of alternative species

are not considered.

Krebs (1973) however, points out that Tinbergen's (1960) formula

$\frac{N_a}{N_o} = \frac{R_a}{R_o} \frac{D_a}{D_o}$ is essentially the same as Murdoch's (1969) formula for the null hypothesis when switching does not occur. The ratio $\frac{N_a}{N_o}$ is the relative occurrence in the diet and $\frac{D_a}{D_o}$ is the relative numbers available. The only difference is that Tinbergen uses the term "relative risk" to describe Murdoch's proportionately constant "C". Krebs furthermore points out that the sigmoid curve can only be obtained where more than one type of prey is present.

Murdoch and Oaten (1975) also state that the formulae are algebraically identical, but emphasise that the hypotheses themselves are different. The difference is most apparent if the density of the main prey is held constant while the alternative prey density varies. In both hypotheses the diet changes because relative encounter rates change. Only in switching however, does the relative risk change as well.

A comparison of the two concepts is complicated by the considerable confusion in the literature as to what the term searching image means. Tinbergen (1960) and Beukema (1968) use the term to denote a change in the predator's ability to see a prey species. The prey are presumably cryptic in such a definition (Krebs 1973). Dawkins (1971) suggests that the term is too imprecise to be useful.

1.2.6 Apostacy

Apostacy is frequency dependent selection in which the predator takes a disproportionately large number of the commoner form in a polymorphic population (Clarke 1962). The concept is equivalent to switching except that morphs rather than different species are considered. Moment (1962) refers to apostacy as "reflexive selection."

The idea that polymorphism may result in lower predation on a rarer morph is quite old (Poulton 1884, Wallace 1889). Fisher (1930) suggested that a balanced polymorphism results when genotypes are selected against

when common and favoured when rare. Haldane and Jayakar (1963) have shown mathematically that apostatic selection equilibrium can arise for two or more genes as long as selection is not too intense. A number of authors have claimed that apostatic selection maintains variability in a polymorphic population (Allen and Clarke 1968, Clarke 1969, Clarke and O'Donald 1964).

Allen and Clarke (1968) demonstrated apostatic selection by wild passerines using artificial prey. The two prey were different coloured pastry "larvae" and the rarer "morph" suffered proportionally less predation than the commoner. Allen (1972) demonstrated apostatic selection with wild blackbirds, Turdus merula, but only at low prey density. At high prey density selection was stabilising.

The advantage for a population being polymorphic could arise from its ability to hide its members in a variety of backgrounds (Huxley 1955) or by providing the predator with several visual "species" which must be learned (Brower 1958). Croze (1970) found that wild crows take fewer individuals when in a polymorphic population than in a monomorphic one. The "morphs" were colour variants of mussel shells with pieces of meat concealed under them. He suggests that failure to form a search image was the cause of the lower predation rate as the birds had more difficulty in finding prey.

1.2.7.1 Holling's type 3 functional response

Holling (1959a) studied the relationship between the density of cocoons of the European sawfly, Neodiprion sertifer, and the proportion it constituted in the diet of three species of rodents. The results of the study indicated that the predators at first responded only slowly to increasing prey density, then responded rapidly, and finally reached a plateau at which no further increase occurred. A sigmoid curve is thus produced which he labelled the "vertebrate" or type 3 response. More than one prey species is required to produce this effect as it results from

the predator concentrating its attack on one species.

An interaction between learning and forgetting by the predator is suggested as the mechanism which causes the sigmoid response (Holling 1965). A predator is considered to have a threshold at which it will react to a prey. If the prey is palatable it "learns a lesson" which decreases the attack threshold. Forgetting however takes place with time and the attack threshold returns to the prelearning level.

If the prey density is high enough learning is faster than forgetting and the attack rate increases. The levelling off in the sigmoid curve to a plateau is postulated to be due to the animal automatically maintaining a varied diet. The alternative less favoured prey also has a threshold of response. It is attacked if the predator does not encounter the favoured prey quickly enough and becomes hungry.

A cumulative process therefore is postulated to operate rather than Tinbergen's idea of a sudden change. It differs from switching in that it essentially involves changes in the density of the preferred prey rather than relative prey abundances.

A type 2 response, which is called an "invertebrate" response, in which the proportion of a prey in the diet increases with density is obtained if only one prey is present (Holling 1959b). A linear rise to a plateau is called a type 1 response and could be shown by filter feeders (Holling 1965). Holling and Buckingham (1976) have suggested a type 4 functional response where there is a measurable decrease in rate of attack when contacts become frequent. Prey defence or inhibition are given as the cause.

1.2.7.2 More recent studies on type 3 functional response.

Hassell et al. (1977) argue against the concept that type 2 functional responses are typical of invertebrates. They suggest that a type 3 response is likely where there is a threshold prey density below which the efficiency of searching by the predator declines. They support this claim with experiments on a number of insect predators.

There is also some evidence against the concept that two prey species are required for a type 3 response. Sigmoidal functional responses have been claimed for copepods (Richman and Rogers 1969, Frost 1975), zooplankton (McQueen 1969) and Stentor (Rapport reported in Murdoch and Oaten 1975). A type 3 response can arise due to an inhibition in feeding and a complete cessation at non-zero concentrations when food supplies are successively diluted (Parsons et al. 1969). A type 2 response is usually found when only 1 prey species is present (Murdoch and Oaten 1975).

A destabilising functional response may be stabilised by a variety of factors. Murdoch (1973) argues that the effect of feeding upon growth and then the feedback of growth upon feeding could have this effect. Switching under many circumstances produces a type 3 response (Murdoch and Oaten 1975).

Spatial heterogeneity may be stabilising (May 1974, Murdoch 1975). If prey are distributed in patches, then an increase in prey density could result in an increase in the length of time a predator spends in a patch. This leads to a reduction in the amount of time spent in transit between patches. The number of prey eaten per unit time should therefore increase. Oaten (1977) and Hassell and May (1974) have produced models which indicate that the addition of transit time can cause a basically destabilising functional response to become stabilising. Murdoch (1977) has presented a similar argument for the situation where a switching predator chooses between prey in two sub-habitats.

CHAPTER 2

2.1 Location of study area

Field observations and cage experiments were conducted in the mangrove forests at Port Adelaide in South Australia. These mangroves, at latitude 35° 30'S, are among the most southerly in the world, although those at Westonport Bay in Victoria at latitude 38° 22'S are further south (Butler et al. 1977a). Only one species of mangrove is found in South Australia and Macnae (1966) has classified it as Avicennia marina (Forst.) Vierh.

At Port Adelaide the mangroves are extensive and the forests have been described as mature (Butler et al. 1977a) with individual trees being 5 to 6 metres high. The locations of the study sites are shown on figure 1 and the low water mark in this area due to the presence of deep channels, is unusually close to the edge of the forests compared to elsewhere in the gulf.

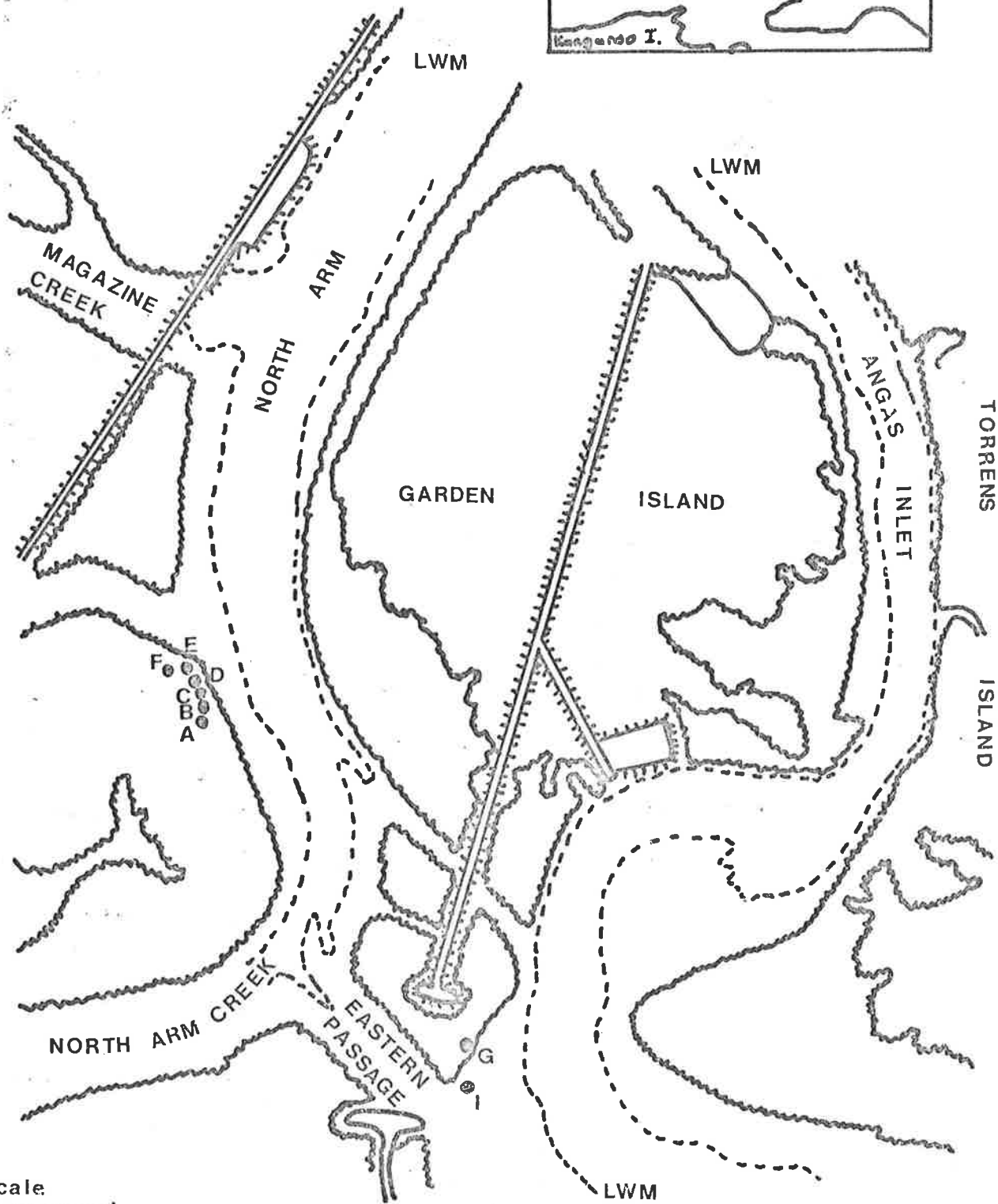
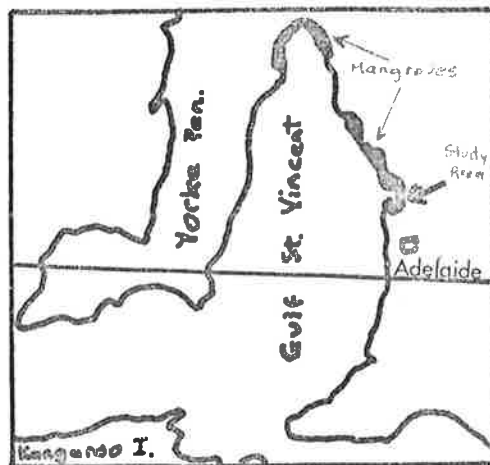
The close proximity of the low water mark to the forest edge reduces the distance which Lepsiella vinosa has to travel across the mud flats to lay its egg capsules and may be a factor in producing the high abundance of this whelk in this area. A short travelling time would reduce the likelihood of encountering predators principally Bedeia paivae on the mud flats. Barnacles are unusually plentiful in this area, presumably due to the favourable conditions created by fast flowing currents in the nearby deep channels.

2.2 General description of the intertidal zone

A diagrammatic representation of the intertidal zone in South Australian mangroves is shown in figure 2 with the range of the principal species examined in this study included. A short description of the animals found in mangroves and on the mud flats in South Australia is given by Womersley and Edmonds (1958) and a comprehensive list of species found in the mangroves is given by Butler et al. (1977b).

Figure 1. Map of the study area. The location of patches A to I is shown.

35



Scale
250 m

The mangroves begin at a height of approximately 1.1 metres above the low water mark and can extend for up to a kilometre inland before the samphires are encountered. The mud flats which are exposed at low tide often consist of sand and shell fragments and extend from approximately 100 metres in the Port Adelaide region to several kilometres further up the gulf.

The section of the intertidal which is of principal interest in this study is the L. vinosa foraging zone. This zone begins at the seaward edge of the mangroves and despite the extremely gradual rise in the level of the forest usually ends about 50 metres inland. Barnacles are most abundant in this zone and are found attached to the aerial roots or pneumatophores and occasionally on low branches and leaves of the trees. Predation on L. vinosa by the gastropod B. paivae appears to prevent this species from foraging on the mud flats and the upper limit of its foraging range appears to be set by the decrease in the frequency of barnacles on pneumatophores further inland. Biotic factors rather than physiological stress thus appear to be of paramount importance in this habitat.

Only those barnacles which settle on pneumatophores are eaten by L. vinosa as the trees are not climbed and thus those barnacles which settle on the branches have a spatial refuge from predation. The distribution of pneumatophores is heterogeneous; patches 2 to 5 metres across containing dense aggregations of tall pneumatophores are often surrounded by areas in which pneumatophores are sparser and shorter in length.

Local drainage patterns and the distribution of mangrove trees are responsible for the production of these patches and the flow of water during each falling tide would favour barnacle settlement and growth. Barnacle density is highest in the pneumatophore patches not only in terms of number per unit

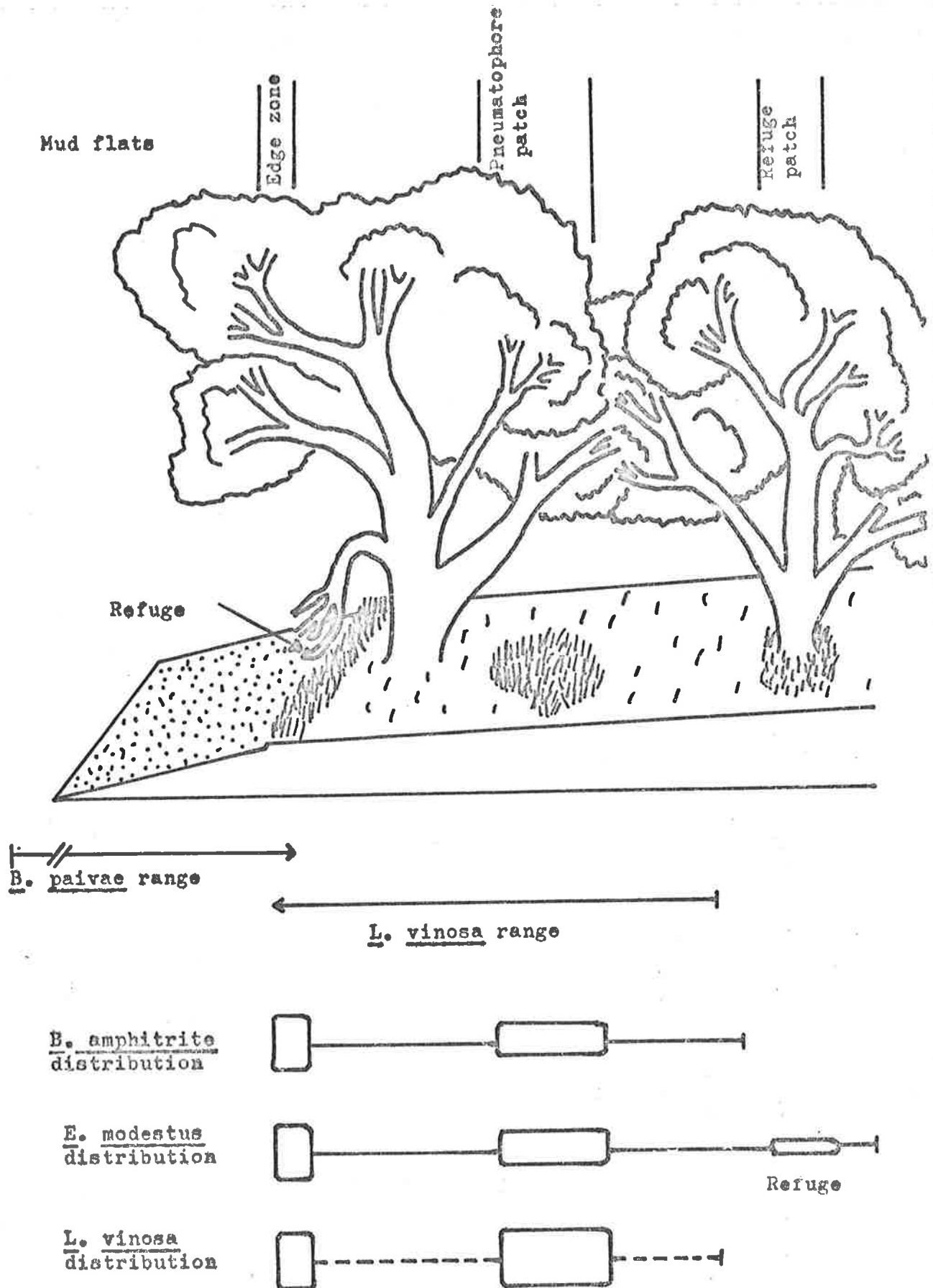


Figure 2. Diagrammatic profile of mangroves with the distribution of barnacle species and predatory gastropods shown.

area but also in terms of number per unit length of pneumatophore. L. vinosa is concentrated in these patches and is rarely observed at low tide on the mud substrate.

The seaward edge of the mangroves is usually characterised by a fringe zone several metres wide of densely packed tall pneumatophores. Heaviest barnacle settlement occurs in this fringe zone and if Balanus amphitrite settlement is very heavy competition can result in the elimination of Elminius modestus. The barnacles in the first metre of this fringe zone are also subject to B. paivae predation. This predatory gastropod migrates upwards from the mud flats and forages on the most seaward pneumatophores and in those seasons in which heavy B. amphitrite settlement occurs they sometimes swarm onto the pneumatophores. L. vinosa is attacked by B. paivae and as a result its foraging is restricted in the most barnacle rich zone in some seasons.

In addition to the heterogeneous distribution of pneumatophores the formation of prey patches is encouraged by the gregarious settling behaviour of barnacles (Knight-Jones 1953). Barnacles prefer to settle where adults are already established and this can result in clumping in homogeneous areas such as oyster grounds (Knight-Jones and Stevenson 1950). The foraging zone is characterised by dense prey patches dispersed throughout an area of prey paucity. These prey patches are restocked during settling seasons. There are few patches more than 100 metres inland and these are usually only colonised by E. modestus and can be considered as refuges because L. vinosa is seldom found.

In years of barnacle scarcity L. vinosa has been observed to attack a small bi-valve, Venerupis crebrelamellata, which is found in barnacle shells, and the herbivorous gastropod Austrocochlea constricta. Salinator solida is readily attacked in the laboratory; Bembicium auratum is only attacked by starved whelks and no examples have been observed in the field. B. auratum would appear to possess too thick a shell for efficient

predation to take place and S. solida is protected by behavioural mechanisms such as burrowing into the mud when immersed and foraging at low tide when L. vinosa is immobilised. Nassarius is far too mobile to be captured by L. vinosa and other molluscs are burrowing forms.



Plate 2. A pneumatophore patch typical of those which were surveyed. A dense aggregation of pneumatophores forms a distinct patch which can be seen in the centre of the plate. Barnacles and L. vinosa are concentrated in these patches.

Some aspects of the prey species.3.1 Introduction

Connell (1970) has suggested that the evolution of a gastropod predator on the upper shore levels is dependent on barnacles being regularly recruited and if the barnacle supply is too variable then no predator can specialise. In the case of L. vinosa in South Australian mangroves two species, B. amphitrite and E. modestus, are available for exploitation and ^{the} whelk feeds on both of them. The availability of new barnacles is determined by settlement patterns, competitive interactions and the variability in annual and seasonal reproductive success of each species. An examination of these factors is likely to give an indication of the feeding problems which the predator had to overcome to adapt to this habitat particularly in regard to prey selection.

3.2 Literature and description of prey species.3.2.1 Balanus amphitrite amphitrite Darwin, 1854 (Previously Balanus amphitrite var. communis).

This is a conical shaped barnacle which is easily distinguished from Elminius modestus by its calcareous base, longitudinal purple stripes on the whitish-grey shell and the presence of six plates in the shell. The thickness of the shell is much greater than in Elminius modestus and it is physically more resistant to pressure.

Darwin (1854) divided the world into five barnacle provinces and stated that this barnacle is found in each province including the Australian. Hoek (1883) recorded its occurrence in Australia, New Zealand, Pacific Ocean, Phillipines, Java, Mediterranean, French Coast, North America, West Indies, Red Sea, Gambia and Madagascar. No earlier records of this species exist and although it may have been spread by shipping prior to the early nineteenth century there is no reason to assume that it is not an Australian species.

Pope (1945) has recorded this species occurring on pneumatophores and trunks of mangrove trees in the Sydney area and states that its range extends from the level of the low water mark of neap tides down to considerable depths. Macnae (1966) and Chapman (1976) state that this species is common on the seaward Avicennia pneumatophores.

3.2.2 Elminius modestus Darwin 1854

This barnacle is easily distinguishable due to its membranous base and its four faintly ribbed grey shell-plates. The shell is by comparison with Balanus amphitrite very fragile and the barnacle is easily broken if removed from the substratum. It is a flattened conical shape which may become tubular in crowded situations.

Darwin (1854) records it from Australia and New Zealand and concludes that it is confined to the Australian province. Hoek (1883) also states that it is restricted to Australia and New Zealand. In the Second World War the barnacle spread to England (Bishop 1947), probably due to the decreased time ships spend in the tropics which enabled its survival in fouling during transport from Australia to England. It first appeared in Holland in 1946 (Boschma 1948) and subsequently spread to Belgium and France (Bishop 1954). It was first recorded in South Africa in 1950 (Sandison 1950).

Pope (1945) describes it as an estuarine barnacle, with a high tolerance of mud and a dislike of wave action, which grows on any type of substratum from the level of high neap tide up to high spring tide mark. In England it has a preference for shallow muddy estuaries (Crisp and Chipperfield 1948). The vertical distribution in England has been examined by Houghton and Stubbings (1963) and found to range from at least 17m to the supralittoral fringe. They suggest that competition with other barnacles resulting in upward displacement may account for the small range given by Pope (1945). Moore (1944) recorded it as occurring intertidally and below low water in New Zealand as did Allen

(1953) in Australia.

3.3 Development of ovaries

In 1976 records were kept on the state of the ovaries and the stage of embryo development for the two species. Samples of 40 individuals of each species were examined. The barnacles were at least 3mm in carino-rostral diameter and in the case of B. amphitrite often larger. Individuals were only examined if they occurred in clumps on the pneumatophores where other adults were nearby as although they are hermaphrodites, cross-fertilisation usually occurs and is only possible if the adults are sufficiently close together (Crisp 1950).

Embryo development was divided into four stages following the classification system of Luckens (1970). The four stages were designated as:-

- A - empty,
- B - eggs in ovary,
- C - immature embryos, that is without eyes, present in mantle cavity,
- D - eyed or mature embryos present in mantle cavity.

The percentage occurrence of each of these stages for the two species is shown in figure 3. All four stages are present in E. modestus throughout the entire year. The continuous presence of mature embryos indicates that this species is capable of continuous breeding although it does not necessarily indicate that nauplius larvae are being released. It is possible for them to be withheld in the mantle cavity for several months if hydrological conditions are not suitable or there is no suitable phytoplankton (Barnes 1957).

Mature embryos in B. amphitrite were only found between mid June and December. The percentage of barnacles with mature embryos was always small compared to E. modestus, and dropped sharply in early October. Examination of B. amphitrite in 1975 however revealed close to 100% of the adults were withholding mature embryos in August and September

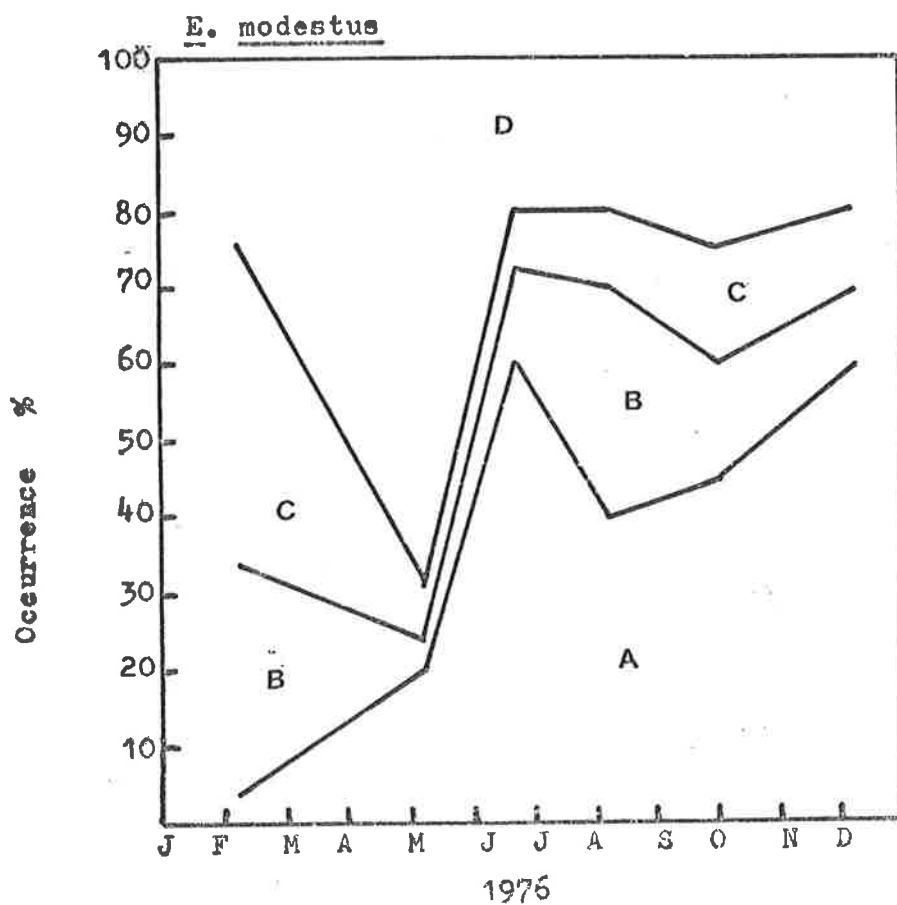
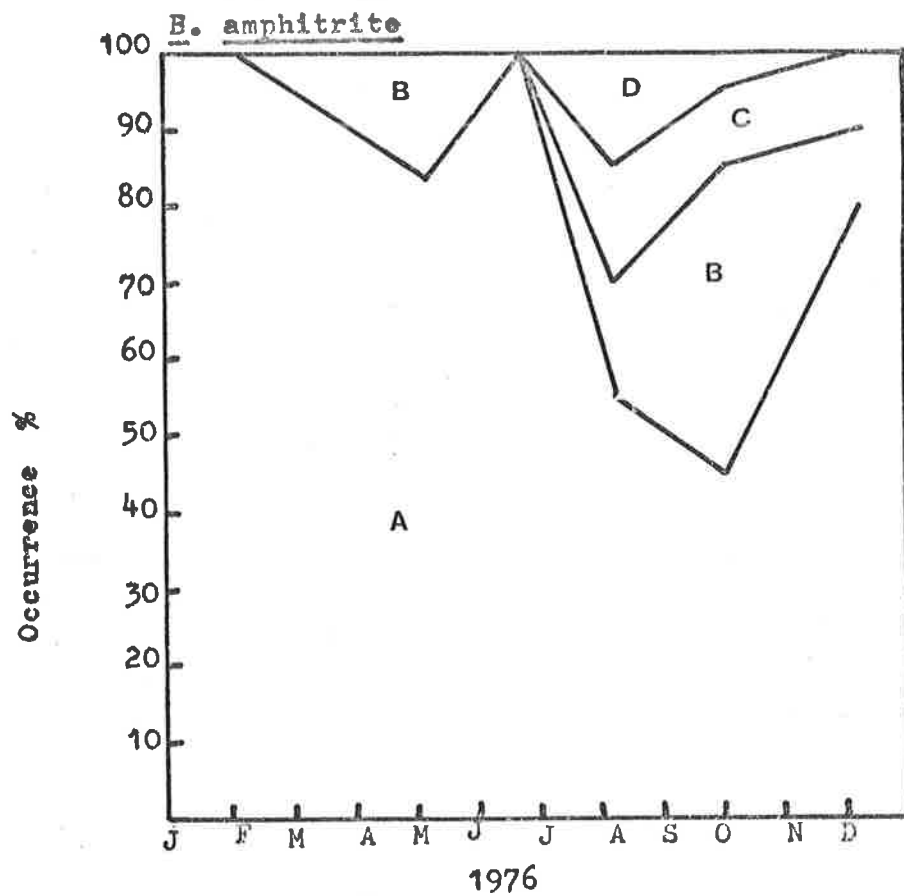


Figure 3. Reproductive condition of B. amphitrite and E. modestus shown as the occurrence (%) of each gonad state in each sample of 40 animals. (February 1976 to mid December 1976).

and the subsequent appearance of only a light spatfall in November was certainly due to a "catastrophe" in the plankton stage. The light spatfall observed in November 1976 however would appear to be due to the failure of embryos to develop in a high percentage of adults and also, more importantly, due to the rarity of adults following the disastrous 1975 settlement.

3.4 Settlement seasons

The settlement seasons of B. amphitrite and E. modestus between September 1974 and March 1976 are shown in figure 4. Rates of settlement in terms of number settling per unit length of pneumatophore are given for individual patches in section 5.1.5.

Heavy settlement of B. amphitrite was only observed in September 1974 and January 1975. The settlement rate in November 1975 was comparatively light compared to the previous year and no significant settlement occurred during the following summer. Settlement appears to be restricted to two short periods, the major one in spring and a second possibly less heavy one in summer. Outside of these periods, small barnacles were rare and usually absent.

Breeding is thus discontinuous and if catastrophic mortality of the larvæ occurs in the plankton, as in spring 1975, then the number of young B. amphitrite settling over a twelve month period is slight. This barnacle can thus be considered to run the risk of having reproductive "failures" in certain years resulting in a marked decline in its numbers in the mangroves which would require several seasons to recover.

Some small E. modestus were found in every month other than June 1975 although few were present between March and July 1975. Settlement outside of this period was always significant and very heavy settlements occurred in November 1975. Breeding is thus almost continuous with a peak period in Spring. This barnacle does not risk reproductive "failures" in certain years and marked variations in its numbers from year to year.

1974

1975

1976

S O N D J F M A M J J A S O N D J F M

B. amphitriteE. modestus

Key



Very heavy settlement



Moderate to light settlement



Very slight settlement

Figure 4. Settlement seasons of B. amphitrite and E. modestus between September 1974 and March 1976.

3.5 Size

The mean carino-rostral diameters of samples of 200 individuals of each species on pneumatophores between December 1974 and March 1976 are shown in Figure 5. Size frequency histograms for B. amphitrite during this period are shown in Figure 6 and for E. modestus in Figure 7.

The mean carino-rostral diameters of B. amphitrite varied from 2.55mm to 5.90mm and were always greater than for E. modestus which varied from 1.55mm to 2.95mm. Individual E. modestus were rarely found larger than 5mm although individual B. amphitrite up to 9mm were found. B. amphitrite is thus the larger barnacle and from the data shown in Figure 8 is capable of growing larger, up to 10mm, in refuges where predation by L. vinosa does not occur. Continuous breeding by E. modestus results in a significant proportion of the population being 1mm or less in size in most samples.

Basal diameters and the heights of the barnacles were not measured in each sample as these dimensions are less convenient to measure and are equally subject to distortions due to crowding and other factors. An adult E. modestus of 4mm carino-rostral diameter would on average be 3mm high and have a basal diameter of 7mm. An adult B. amphitrite of 4mm carino-rostral diameter would on average be 4mm high and have a basal diameter of 7mm. In general E. modestus is more flattened than B. amphitrite although in crowded situations it becomes tubular.

3.6 Refuges

L. vinosa is restricted to pneumatophores for foraging and does not climb trees in search of barnacles. Settlement of barnacles on branches and leaves which are inundated at high tide leads to the formation of spatial refuges in which the prey are free from predation.

Low lying branches of Avicennia are often very close to the tops of pneumatophores and where barnacles have attached to both it is possible to compare a population which has been subjected to L. vinosa predation with a refuge population. The submergence time for each population is

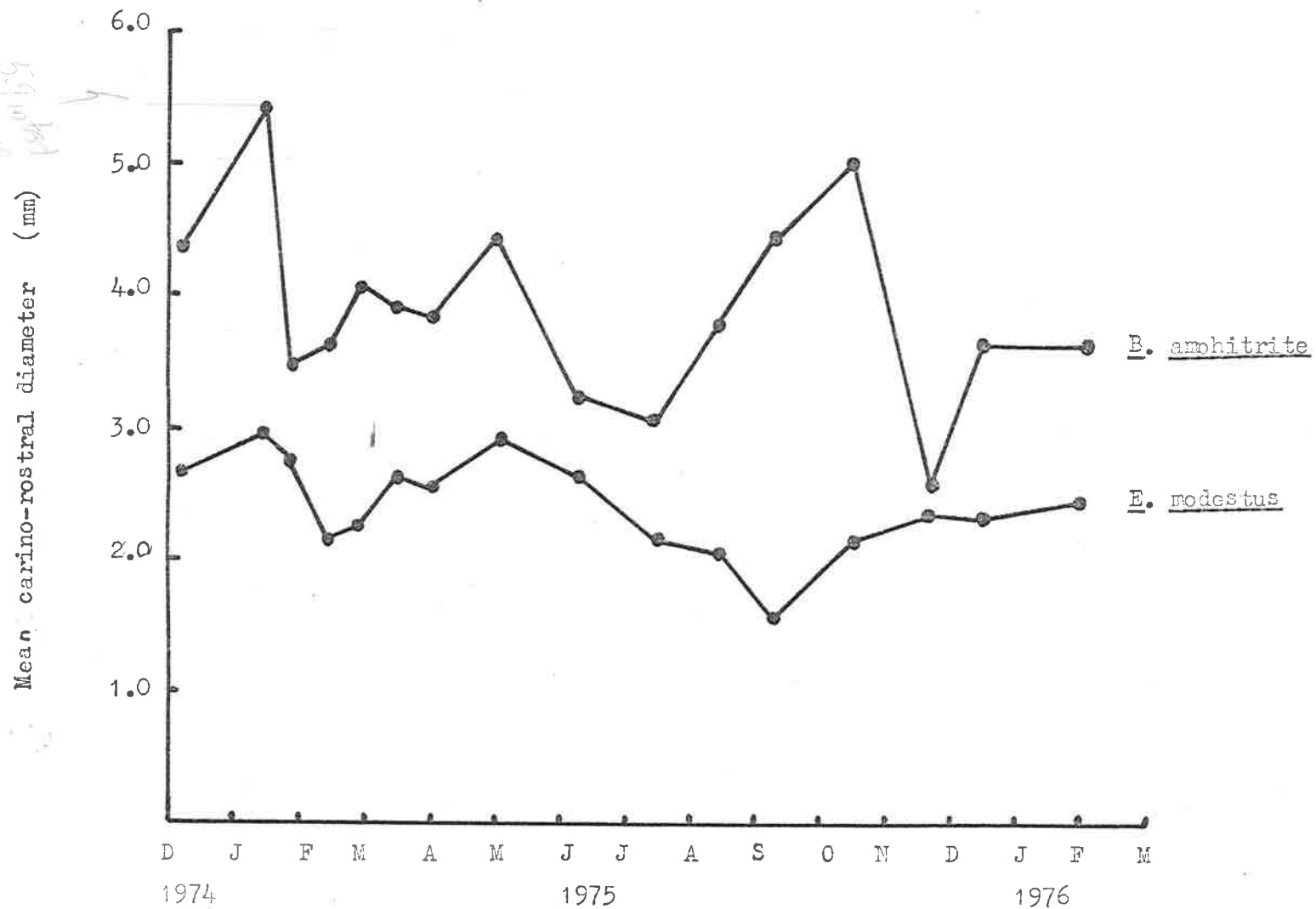


Figure 5. Variation in the mean carino-rostral diameter of samples of 200 B. amphitrite and E. modestus between December 1974 and March 1976.

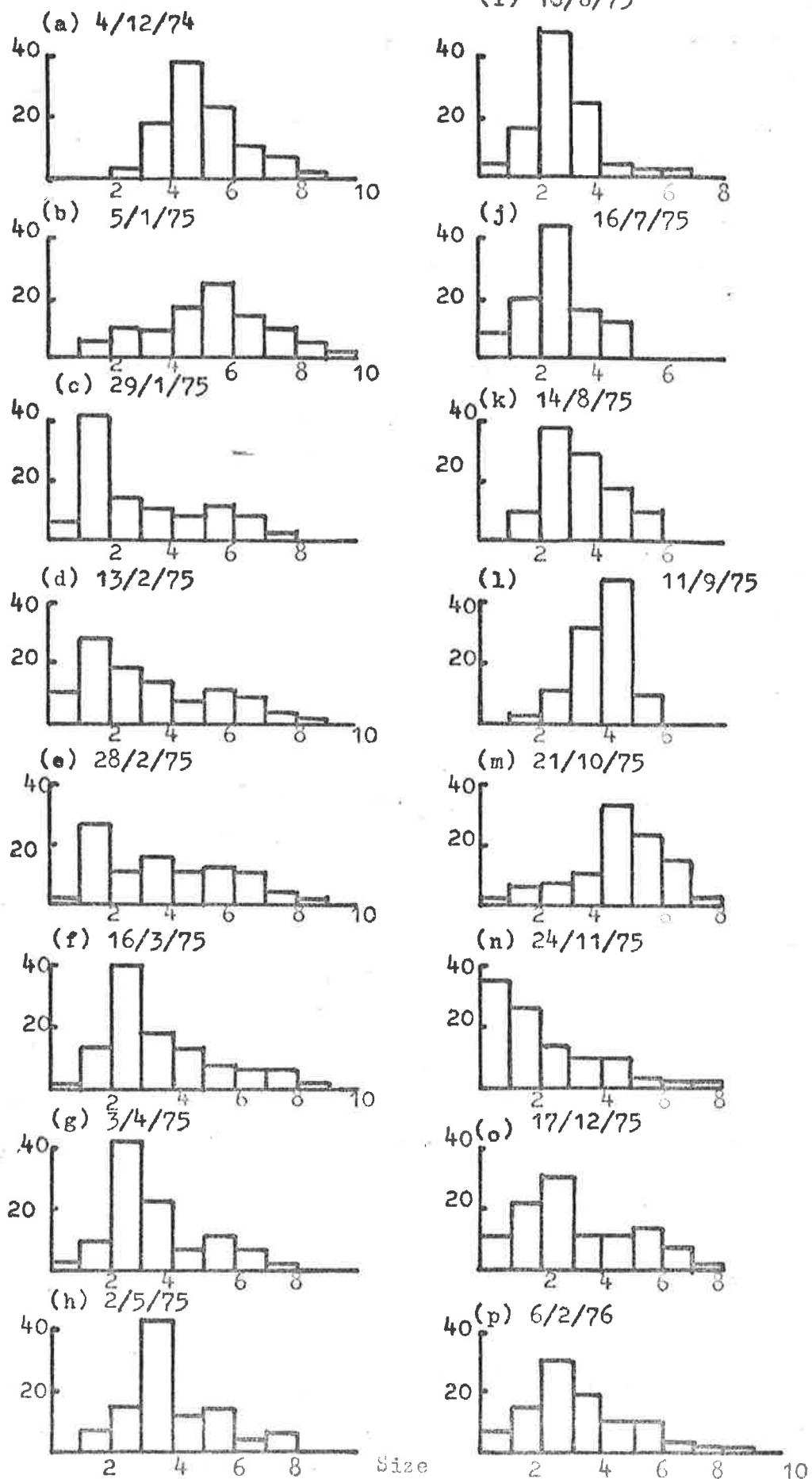
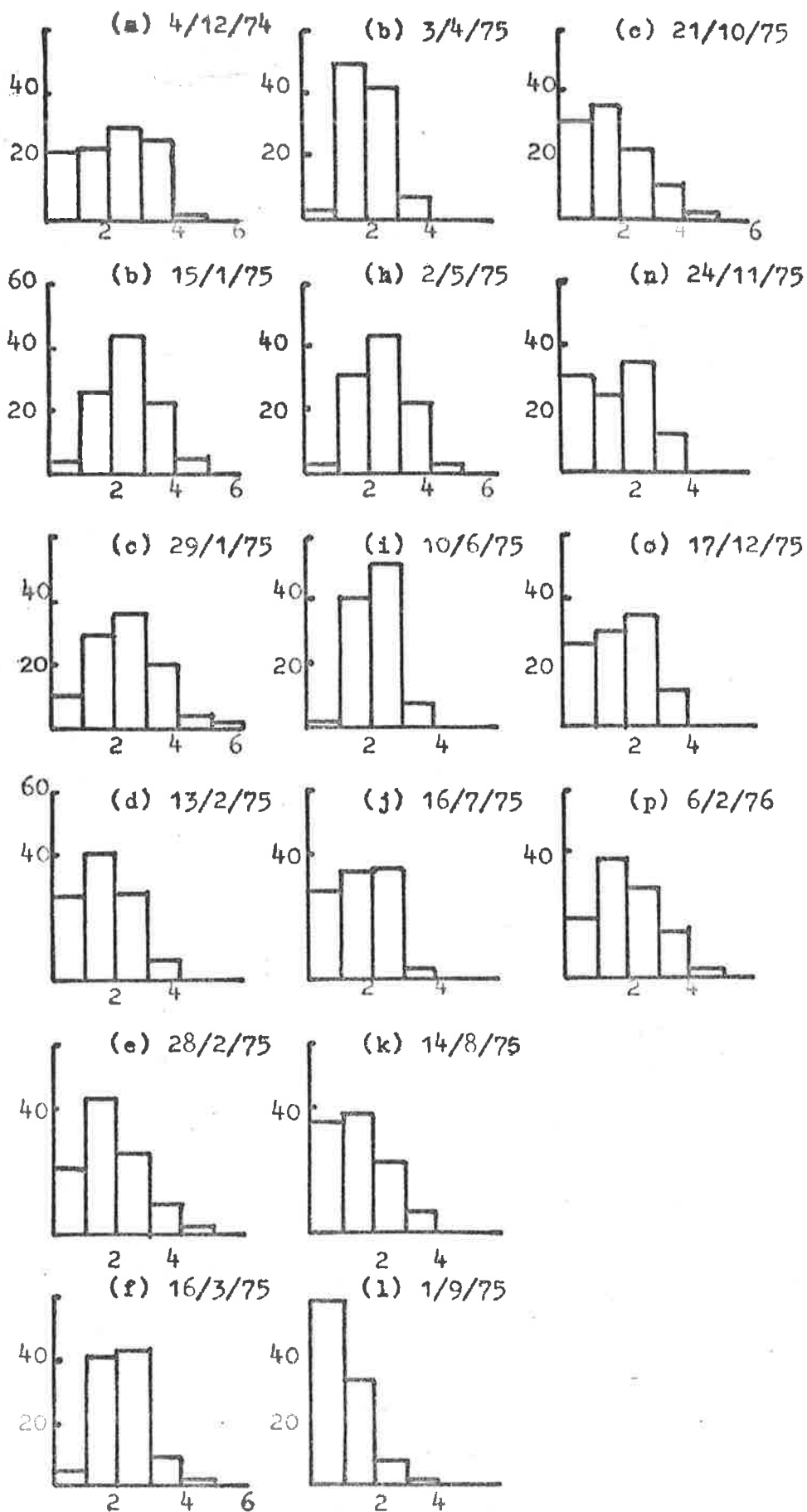


Figure 6 (a)-(p). Size frequency histograms of samples of 200 *B. amphitrite* found on pneumatophores between December 1974 and February 1976. The size is the carino-rostral diameter in mm.

Figure 7 (a)-(p). Frequency histograms of the carino-rostral diameters of samples of 200 E. modestus found on pneumatophores between December 1974 and February 1976.

Frequency



Size (mm)

similar and hence growth rates should be the same. If either population is favoured with respect to growth then it should not be the slightly higher branch population.

It is not possible to be certain of the cause of mortality in the barnacles as L. vinosa always drills through the opercular valves which become dislodged from the remaining shells which are firmly cemented to the substratum. Nevertheless L. vinosa is the most conspicuous predator which is confined to only one population and there are no other apparent causes of differential mortality. The fragile E. modestus often becomes detached after dying and as a result only the firmly cemented B. amphitrite could be examined.

The ratio of dead to living B. amphitrite in the refuge was 0.53 whereas on the pneumatophores it was 11.74. This ratio gives an indication of the greater mortality on pneumatophores and suggest that L. vinosa has a marked influence on barnacle survival.

Size frequency histograms of dead and living B. amphitrite in the pneumatophore patch and on the branch are shown in figure 8. In table 1 the means and ranges of the carino-rostral diameters are listed.

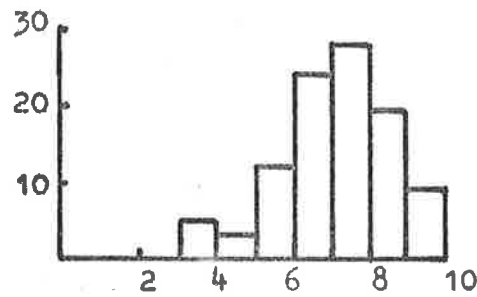
TABLE 1 Carino-rostral diameters of B. amphitrite in a refuge and on nearby pneumatophores.

		n	$\bar{x}$	range (mm).
Pneumatophores:	Living	40	5.4	4-7
	Dead	100	4.6	2-8
Refuges:	Living	100	7.6	4-10
	Dead	100	7.5	5-10

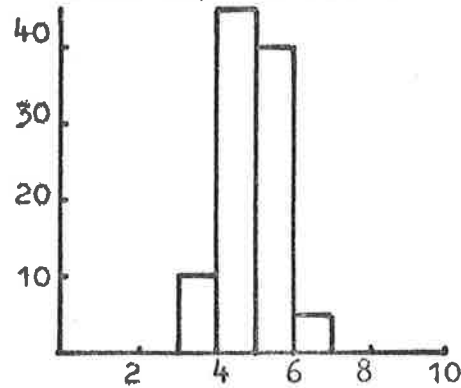
A statistical analysis of the carino-rostral diameters of dead and living B. amphitrite in the refuge and on the pneumatophores is shown in Table 2. The sizes of the shells in each case were compared using an ordered contingency table (Goldstein 1964).

(a) Living B. amphitrite

Refuge population

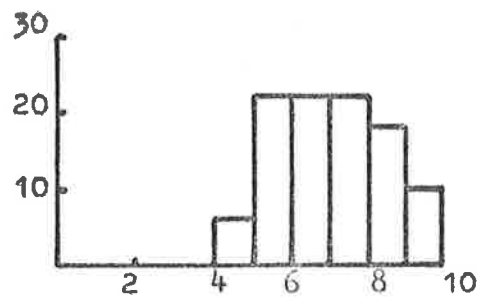


Pneumatophore population

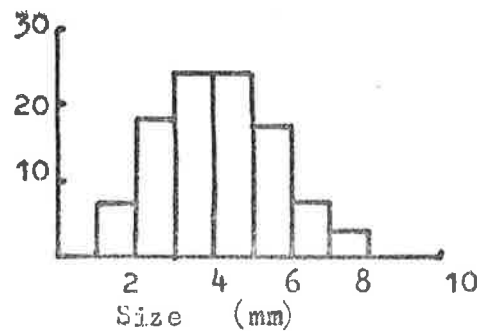


(b) Dead B. amphitrite

Refuge population



Pneumatophore population



Frequency

Figure 8. Frequency histograms of the carino-rostral diameter of living B. amphitrite (a) and dead B. amphitrite (b) in refuges and on pneumatophores. (August 1977)

TABLE 2 Comparison of carino-rostral diameters of B. amphitrite in predator free refuge and predator infested pneumatophore patch.

Pneumatophores and refuge:	Living barnacles	x*	4.0	significant
	Dead barnacles		13.3	significant
Living and dead barnacles:	Refuge		0.47	not significant
	Pneumatophores		25.5	significant

The results show highly significant differences in the size structure of refuge and pneumatophore barnacle populations. The refuge barnacles are much larger and are survivors from the 1974 spring settlement which were all eliminated within 3 years on the pneumatophores. The difference between the size of living and dead barnacles in the refuge was not significant and this indicates that unlike the pneumatophore barnacles death was occurring among fully grown adults. The significantly different size structure of the dead barnacles between the refuge and pneumatophores also indicate a lower life expectancy in the L. vinosa predation area.

3.7 Competition

3.7.1 Interspecific

Competition, resulting in the elimination of one species of barnacle by another species, has been demonstrated using controlled field experiments by Connell (1961). In this study B. amphitrite was observed to eliminate E. modestus in crowded situations due to its larger size and stronger shell.

Crushing is by far the most common cause of E. modestus mortality in crowded situations. Undercutting and lifting off the substratum is less common and smothering is fairly rare. E. modestus possesses an extremely fragile shell and has no capacity to eliminate B. amphitrite or to resist the pressure exerted by growing barnacles of this species.

3.7.2 Intraspecific

In barnacles intraspecific competition can lead to mortality due to smothering, crushing and hammock formation which results in unstable

attachment to the substratum. Thick clumps of barnacles are vulnerable to removal by wave action during storms and this has been reported to result in the elimination of whole populations from local areas (Barnes and Powell 1950). Detachment of barnacle clumps can be considered as a form of delayed mortality due to crowding (Connell 1961).

B. amphitrite forms clumps which could be less stable on pneumatophores than individually attached barnacles. Hammock formation does not occur with E. modestus. Smothering of underlying barnacles by the members of the same species was observed in B. amphitrite clumps.

Mortality due to crushing and undercutting was rare for B. amphitrite aggregations. Lateral crushing in E. modestus aggregations was common and the barnacles were often tubular and distorted in shape. Crowding in E. modestus has been reported to lead to smaller individuals which are slow to mature (Crisp and Davies 1955).

3.8 Discussion

In a spatially static situation B. amphitrite will beat E. modestus in competition for space provided that the density of settlement is sufficiently high. Nevertheless the short generation time and continuous breeding of E. modestus gives this barnacle the ability to co-exist with B. amphitrite. E. modestus takes only 8 weeks, and possibly less in summer, from settlement to reach maturity. Given a planktonic life of 4 weeks (Crisp and Davies 1955) the generation time is 12 weeks. B. amphitrite may however require a full year between generations.

It has been suggested that superior dispersal and reproductive capacity could enable a hypothetical plant species to co-exist with another which is superior in competition (Skellam 1951). Hutchinson (1951) developed a similar concept from a consideration of copepod species and termed the weaker competitive species which can only survive by a good dispersal mechanism a "fugitive" species. An equilibrial theory for such fugitive populations was developed by Horn and MacArthur (1972)

and they conclude that sufficiently high migration among patches by a competitively inferior species can result in stable co-existence instead of competitive exclusion.

In crowded situations L. vinosa prefer B. amphitrite to E. modestus and it could be expected that the effects of predation would lessen interspecific competition by eliminating the superior competitor. Connell (1961) found that intense predation could prevent competition for space in the intertidal zone.

As far as can be ascertained from the literature the B. amphitrite - E. modestus interaction was not recently established in South Australia. The "export" of E. modestus to Europe has led to the formation of similar interactions with European Balanus species (Houghton and Stubbings 1963, Crisp and Davies 1955). The adaptation of L. vinosa to the mangroves has required the predator to adapt to this interaction and it can be argued that this is a co-evolved predator prey association.

Barnacles which have only one breeding season are vulnerable to catastrophes which can destroy the entire year's settlement. The English barnacle Balanus balanoides has only one breeding season and over a period of up to ten years has been observed to have "failure" years in which few have settled (Barnes 1956, Connell 1970). Barnes (1957) demonstrated that this species held its larvae within its mantle cavity until the beginning of the spring phytoplankton bloom of diatoms upon which they feed. Abnormalities in the diatom outburst is believed to cause the death of the cyprids in some years as they cannot utilise dinoflagellates as a food source (Barnes 1957, Moyse 1963).

In this study the failure of B. amphitrite to settle in significant numbers in spring 1975 was ^{apparently} due to mortality of larvae in the plankton. This resulted in a serious depletion in this species' numbers in the mangroves from which it has not recovered in 1976 and 1977. The gonads of a high proportion of the barnacles did not develop in 1976 and this

further reduced the possibility of a recovery. These barnacles were mainly two years old compared with the previous breeding seasons which consisted of one year olds. Possible reasons for this low rate of larval development could include parasitism which has been shown to prevent gonad development although not visibly affect the barnacles appearance otherwise (Crisp and Davies 1955). Barnacles are also believed not to produce as many larvae in second and later years after the first breeding season (Moore 1958).

Connell (1970) argues that unless the supply of barnacles in the high intertidal is adequate and regular a whelk will not evolve for that location. The irregular settling pattern, years in which the breeding can be considered a "failure" and the tendency for population crashes makes it unlikely that L. vinosa could have colonised the mangroves of South Australia, as a feeder on B. amphitrite. It is probable that the presence of E. modestus as a food source was necessary for it to make the transition from rocky shores to mangroves. Like the rocky shore population the mangrove whelks have their young emerging from egg capsules in May which is at least three months prior to the spring B. amphitrite settlement. The only small barnacles available at this time are E. modestus.

Prey species which have reproductive failures in some years can be expected to have an extremely marked effect on their dependent predators population numbers. May (1973) states that a predator population reduced from its equilibrium value by the reduction of its prey population will, due to the dynamics of the system, be further reduced and the prey can be expected to subsequently increase in abundance beyond its original equilibrium value. Smith (1970) examined the effect of some species of conifers having years in which cone production failed on their dependent pine squirrels. He found that the reduction of the squirrel population and the lowered predation rate in subsequent years more than offset the loss of the cones in one year. Nevertheless the conifers put the energy saved from cone production into vegetative growth whereas

failures in barnacle breeding cannot be additionally utilised in this manner.

The slow recruitment of new whelks into the mangroves would mean that a B. amphitrite dependent predator would not be very successful. This argument could be extended to feeding morphs, that is the abundance of the B. amphitrite eating morph would be very low compared to an E. modestus eating morph. Indeed the dynamics of this barnacle system would not favour the formation of feeding morphs at all. A successful predator in this system would be one which during its long life, that is many years, could utilise E. modestus and at the same time be capable of changing to the preferred prey, that is B. amphitrite, if it became abundant.

Slobodkin (1961) states that in the absence of refuges predator prey interactions are unstable. Connell (1970) found that Thais ate every barnacle within 2 years after attachment below refuge areas and suggest that refuges may always be required for persistent predator prey interactions. Flatworm predation has also been found to completely destroy barnacles which are not in a refuge (Hurley 1976).

5/ The largest 56% of B. amphitrite in the refuge population examined in this study would have been at least 3 years old and no barnacles on the pneumatophores reached this size. This indicates that L. vinosa is capable of eliminating, within the following 3 years, all barnacles which settle even during a successful year. Pneumatophore death would also reduce the survival period of a proportion of the barnacle population and this will be discussed in section 5.1.4. Branches can be expected to be long-lived although leaves which are often colonised by E. modestus could only form a short-lived refuge, but, probably of sufficient duration for one generation of larvae to develop and be released.

For the prey species the problem with refuges is that although they provide protection from the predator they are in general inundated by high tides less often and for shorter periods than in non-refuge areas. The

refuge may thus not be located at the height in the intertidal zone which is physiologically optimal for the species. This may result in slower growth (Connell 1961, Hatton 1938, Barnes and Powell 1953, Hatton and Fischer Plette 1932), less gonad development (Moore 1935 and 1934), shorter breeding seasons (Crisp 1950, Luckens 1968), problems restocking by new settlement (Connell 1970) and the increased risk of desiccation and death during hot weather (Hatton 1938, Connell 1961). Desiccation resistance however can be expected to increase with size (Foster 1971).

The ability of a species to breed continuously in the high intertidal zone confers a further advantage over a competitively superior species which has the same physiological requirements and settling range. Foster (1971) has suggested that the long breeding season of E. modestus in England gives it a greater chance of settling, growing and surviving high on the shore as successful establishment is dependent on the chance occurrence of favourable weather conditions. Barnacle patches in South Australian mangroves which are farthest from the seaward edge often consist solely of E. modestus. Refuges on trees are also more often settled with E. modestus than with B. amphitrite.

CHAPTER 4

Some aspects of the feeding behaviour of *Lepsiella vinosa*.

4.1 Introduction

Lepsiella vinosa is normally described in the literature as a rocky shore species which eats mussels, serpulids and barnacles (MacPherson and Gabriel 1962, Wilson and Gillett 1971). It is found from southern New South Wales to Western Australia and also in Tasmania (Coleman 1975).

In this chapter a number of aspects of the feeding behaviour of *L. vinosa* are presented. These aspects are the prey evaluation behaviour, the effect of pure diets of one prey species on growth and the influence of season and prey abundance on the feeding rates in the field.

4.2 Prey evaluation

L. vinosa do not attack every barnacle they come into contact with and reject many potential prey items after thorough examination. Observations of the prey evaluation behaviour were made in aquaria in which *L. vinosa* were provided with pneumatophores with barnacles on them.

L. vinosa move slowly along the length of a pneumatophore and make initial contact with a barnacle with the tentacles. It then climbs onto the opercular valves and usually orientates along the slit between the scuta and terga. A series of rotations, usually to 90° although sometimes to 180° from the original position, follow. After each change of position a series of pulling and rocking motions take place.

In table 3 the time *L. vinosa* required to evaluate a barnacle before rejecting or before becoming stationary in the case of a barnacle selected for drilling is shown. Three out of every four barnacles were rejected. Evaluation prior to rejection took an average 3.9 minutes and usually consisted of two rotations with pulling and rocking actions at each position.

TABLE 3 Time L. vinosa spent in evaluating a barnacle.

	<u>Number of observations</u>	<u>Mean time</u> <u>(Minutes)</u>	<u>Range</u> <u>(Minutes)</u>
1. From initial contact to rejection:	12	3.9	1.8-7.25
2. From initial contact till final drilling position assumed.	4	19.5	17.0-22.0

L. vinosa which attacked a barnacle spent an average 19.5 minutes evaluating the barnacle prior to assuming the final drilling position. In this time up to 10 rotations with pulling and rocking actions following each change of position took place. The whelks drill into the scuta over the abductor mussel. It is possible that the strength of the abductor mussel is assessed by the pulling and rocking actions.

4.3 Growth rate of L. vinosa on pure diets of each prey species.

The comparative suitability of prey species as a source of food for a predator can be assessed by the growth and mortality of the predators on pure diets of each species, assuming any single species is adequate as a complete diet. If a prey species does not satisfy the nutritional demands of the predator then a reduction in the growth rate and possibly mortality should be observed. L. vinosa does not die under laboratory conditions from starvation even if kept without feeding for eight months and therefore comparative mortality rates are not useful.

The suitability of each prey species as a food source was determined by feeding juvenile L. vinosa on pure diets for eight weeks and measuring the increase in shell length. The whelks were measured with vernier calipers from the apex to the tip of the anterior canal. They were then individually numbered and placed in aquaria. Each aquarium had a large number of barnacles in excess of the whelks' feeding requirements, with only one prey species present. The prey were replaced weekly and showed little mortality from causes other than predation. A control aquarium was set up in which L. vinosa were not fed. Aquaria were kept at room temperature.

The results obtained are listed in table 4 and the mean growth rate is similar for each diet. There is no significant difference on the basis of a Mann-Whitney U test ($U=105.5$, $N=16$, $N'=13$). In each case a number of L. vinosa showed no growth at all.

The experiment was run from 6/7/77 to 1/9/77 which includes the coldest time of the year. Most of the growth was in August and very little growth was observed in July when the water temperature was low. A higher growth rate would be expected in summer and it is possible that differences in growth would become apparent under conditions of increased metabolic activity. Luckens (1970) however found that Ocenebra japonica, in mid summer, increased 7.4mm in length over a two month period irrespective of whether the whelk was fed Mytilus or barnacles. The barnacles were the preferred prey species. It must be concluded that prey preference is not necessarily reflected in comparative growth rates.

Growth in laboratory aquaria can be expected to be higher than in the field as there is continuous submergence leading to continuous feeding and an over-abundance of food (Feder 1970, Luckens 1970). Growth rates under laboratory conditions have been found to be reduced by gonadal maturation (Paul et al, 1977) but this should not occur in L. vinosa in July and August.

TABLE 4 Growth of juvenile L. vinosa fed for 8 weeks on diets consisting of purely one species of barnacle.

Diet	Number of <u>L. vinosa</u>	Mean Size	Mean Growth	Standard Error
Pure <u>B. amphitrite</u>	16	13.15mm	1.10mm	0.03
Pure <u>E. modestus</u>	13	13.85mm	1.04mm	0.03
Control (not fed)	11	14.48mm	0mm	-

4.4 Feeding rate of L. vinosa in barnacle patches

4.4.1 Introduction

The feeding activity of marine invertebrates, particularly gastropods

and starfish, can be quantified in the field by turning the animals over and scoring the number feeding and the number not feeding (Paine 1969), Feder 1970, Menge 1976). In most of the surveys on prey selection records were kept of the number of whelks not feeding as well as the number feeding. It is possible to determine a percentage of whelks feeding during these surveys and relate this feeding rate to season, patch and prey density. Feeding rates estimated as the number of barnacles consumed ~~per~~ whelk per week are given in section 9.3.7.

4.4.2 Influence of season

The percentage of whelks feeding in each month is listed in Table 5 and the mean values and standard errors are shown in figure 9. The wide range of values for most months make it difficult to determine whether there is a seasonal trend. The mean values are lowest in the two coldest months, June and July, possibly indicating a lower feeding rate in this period. Nevertheless there is no seasonal cessation of feeding.

L. vinosa is at the northern extremity of its distribution and cessation^{of} feeding in the coldest months is less likely than in colder areas. Latitude has been found to effect the seasonal trend in the feeding of Pisaster ochraceus. In Monterey Bay, California, it feeds without seasonal trends (Feder 1970) although further away from the equator at Puget Sound, Washington, it has seasonal changes in feeding rate (Mauzey 1966, Paine 1969). Christensen (1970) says that the sea star Astropecten irregularis stops feeding when the temperature drops below 4°C and peaks in summer. Hanks (1957) examined the feeding rate of Urosalpinx cinerea and found it did not feed if the water temperature was below 7.5°C . Its feeding rate increased from 10°C to 25°C then decreased to 30°C which was the upper limit.

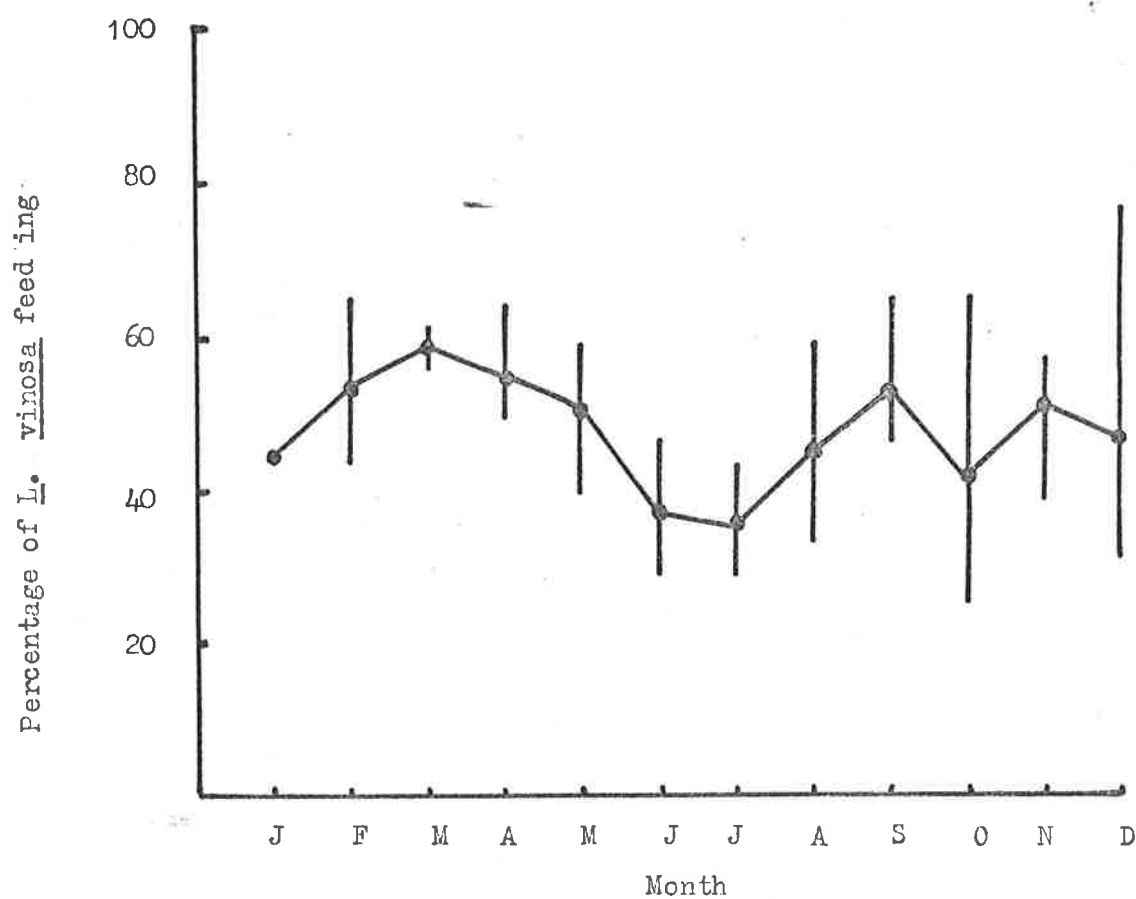


Figure 9. Percentage of *L. vinosa* observed feeding in different months. Vertical lines indicate the range and the means for each month are shown (●).

TABLE 5 Percentage of L. vinosa observed feeding during each month.

<u>Month</u>	<u>Mean Percentage</u>	<u>(S.E.)</u>	<u>Number of Observations</u>	<u>Range</u>
Jan.	44.0	-	1	-
Feb.	53.3	(6.5)	3	43.3-65.4
Mar.	58.3	(1.7)	3	55.2-61.0
Apr.	54.3	(4.9)	3	48.8-64.1
May.	50.6	(6.0)	3	39.0-59.4
June	36.8	(5.3)	3	28.1-46.4
July	35.0	(3.4)	4	28.2-42.9
Aug.	44.7	(3.3)	8	33.3-59.6
Sept.	52.8	(3.0)	6	45.8-65.0
Oct.	41.2	(4.3)	8	24.3-65.2
Nov.	50.6	(5.8)	3	39.0-56.7
Dec.	46.0	(7.0)	6	31.0-76.7

4.4.3 Influence of patch

The mean feeding rate for the patches A,B,C,D,E, and F during the period of observation was 45.19 ($\pm$ 1.87 S.E.) percent feeding. The mean values for G and I patches were not included as in many surveys no record was kept of new animals which were not feeding. Although the density of barnacles was extremely high at some times, there did not appear to be a much higher feeding rate than that which was observed in the six inland patches. The percentage of L. vinosa feeding in each patch is listed in Table 6 and the similar values indicate that the differences in relative and absolute barnacle densities did not have a marked effect.

TABLE 6. Percentage of L. vinosa observed feeding in each patch.

<u>Patch</u>	<u>Mean Percentage</u>	<u>(S.E.)</u>	<u>Number of Observations</u>	<u>Range</u>
A	47.2	(3.8)	11	30.8-65.2
B	48.6	(4.1)	11	25.0-65.4
C	41.0	(3.4)	11	24.3-65.0

Table 6 cont.

<u>Patch</u>	<u>Mean Percentage</u>	<u>(S.E.)</u>	<u>Number of Observations</u>	<u>Range</u>
D	45.1	(6.4)	3	33.3-55.3
E	43.7	(8.4)	3	27.3-55.0
F	42.0	-	2	38.1-45.8
All patches	45.19	(1.87)	38	24.3-65.4

4.4.4. Influence of prey abundance

The influence of the availability of prey on feeding rate is shown in figure 10 and the values listed in Table 7. There is no significant correlation of feeding rate with prey density ($R_s = 0.217$, $t = 1.35$, $df = 37$, $P > 0.05$). This indicates that the prey densities in the patches are sufficiently high for normal feeding.

TABLE 7 Percentage of L. vinosa feeding at different prey densities.

<u>Prey density</u> <u>No. prey/metre</u>	<u>Mean</u> <u>Percentage</u> <u>feeding</u>	<u>(S.E.)</u>	<u>Number of</u> <u>Observations</u>	<u>Range</u>
5-10	30.8	-	1	-
10-15	42.5	(5.6)	6	24.3-56.3
15-20	42.7	(4.0)	11	25-65.2
20-25	40.1	(5.9)	3	28.6-48.3
25-30	48.2	(3.8)	8	33.3-65.4
30-35	44.8	(4.7)	3	39.0-54.0
35-40	42.9	-	2	35.8-50.0
40	49.9	(3.9)	5	38.1-57.6

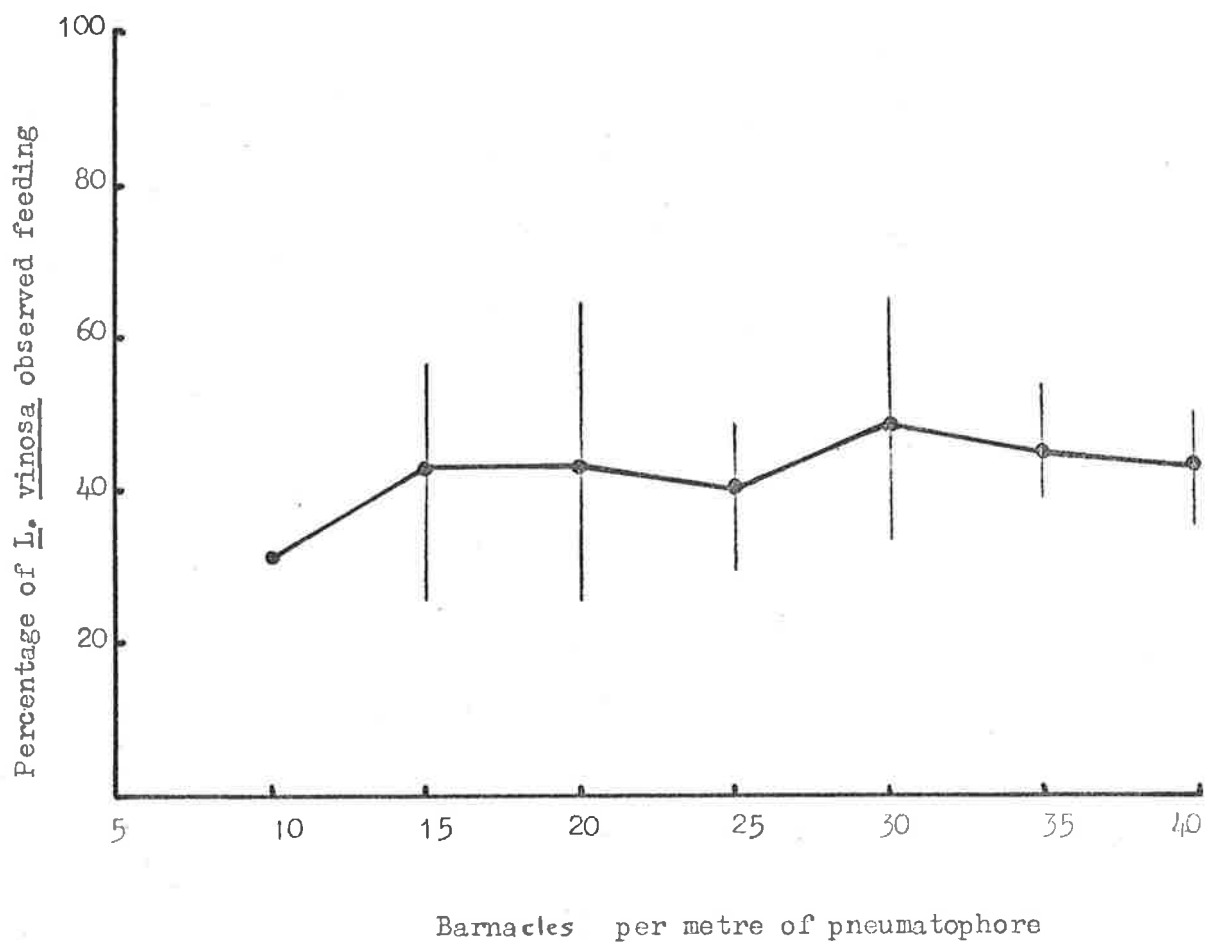


Figure 10. Percentage of *L. vinosa* observed feeding at different prey densities. Vertical lines indicate the range and the means are shown (●).

CHAPTER 5

Dynamics of barnacle populations in pneumatophore patches.

5.1 Inland patches

5.1.1 Introduction

The dynamics of barnacle populations on rocky shores has received considerable attention in the literature. The influence of physical and biological factors regulating zonation have been investigated by Connell (1961a,b) in Scotland and Luckens (1975) in New Zealand. The roles of invertebrate predators in causing the survival or elimination of barnacle species in intertidal communities have been investigated by predator inclusion and exclusion experiments by Paine (1966) and Dayton (1971). The relative effect of gastropod predation and competition between species on the survival of Balanus glandula has been assessed by Connell (1970). Hurley (1975) examined the elimination of a sub-tidal barnacle population by a Turbellaria predator.

The interaction between the barnacle populations and L. vinosa in pneumatophore patches is examined in this chapter. A unique feature of this system is that the only solid substrate is provided by living pneumatophores which alter with time as individuals grow, die and are replaced. New pneumatophores provide a new source of bare substrate for settlement whereas on a rocky shore prey death and removal is required. Pneumatophore death is a new source of mortality as the substrate on which barnacles are normally studied is inert. The general dynamics of the pneumatophores can result in increasing or decreasing quantities of substrate in the patches and it is as a result impossible to study the dynamics of the prey populations without examining pneumatophore dynamics as well.

Unlike rocky shore studies quantitative sampling requires the permanent removal of substrate and the attached barnacles and this introduces potentially large experimenter influences. Falk (1974) has emphasised that in studies in which sampling procedures involve the

removal of organisms there is a possibility of the experimenter biasing the result. This bias should be quantified where possible. Techniques normally used on rocky shores, such as photographing marked areas of substrate, are not possible. Individual barnacles could not be followed and the estimation of barnacle densities cannot be expected to be as accurate.

5.1.2 Sampling procedures.

Three inland patches were surveyed between February 1975 and February 1976 at intervals varying from two weeks initially to up to six weeks at the end of the study. Results obtained from another three inland patches and also the typical edge zone were not included in this section as they were primarily collected to determine the prey selectivity of the predator. The results of an atypical patch on a small island, unusually low in the intertidal, will be treated separately as this area was principally subject to B. paivae predation and was not an example of a normal L. vinosa foraging patch.

Patches were surveyed to obtain as complete an assessment of what was going on as possible. A random sample of pneumatophores was collected by throwing a leaf into the patch and cutting the five nearest pneumatophores off at their base. Initially a total of 20 pneumatophores were removed per survey, but as the barnacle density decreased the sample size was increased to about 50 as the ratio of barnacle species was an important consideration. From these pneumatophores the number of living B. amphitrite and E. modestus were counted as well as the number of dead B. amphitrite. The pneumatophores were measured and in the larger samples an estimate of those present since the end of summer 1975 was made by examining the barnacles. Those pneumatophores with old and dead B. amphitrite could be assumed to be old and those which had no B. amphitrite and were short in length could be considered as new.

The density of pneumatophores was estimated by taking 5 random quadrats of 33x33cm. The average number of pneumatophores in them was multiplied by

9 to give density in terms of number per square metre. The area of patch A was 9.2 square metres, patch B was 3.5 square metres and patch C was 9.5 square metres.

An attempt was made to find all whelks which were after marking returned to the patch. Records were thus kept of the number of whelks in each patch at each survey.

From these samples it is possible to keep records of the following parameters for each patch; barnacle density of each species expressed per unit length of pneumatophore or unit area of patch, pneumatophore density of both new and old pneumatophores per unit area of patch, changes in pneumatophore mean length, the ratio of dead to living B. amphitrite, barnacle size and the number of predators present.

5.1.3 Experimenter influence

An unfortunate feature of this field study is the extent to which experimenter influences affected the prey patches and became a major element for consideration in assessing the dynamics of the prey. To some extent they could be quantified, and where possible this has been done, although there are also a number of unquantifiable aspects.

Certain aspects of sampling led to the destruction of areas of the patches. The cutting of pneumatophores in sampling is a directly quantifiable aspect and the effect on both substrate and barnacle populations can be determined. In table 8 the number of pneumatophores and their associated barnacles which were removed at each survey are given. The percentage of the old pneumatophores removed during the study by sampling is included in figure 13. The effect of sampling on the number of B. amphitrite surviving from summer 1975 to 1976 in the three patches is included as a factor in figures 21 to 23.

From these figures it is apparent that direct sampling was most deleterious to patch B. This is because equal numbers of pneumatophores were removed from the patches although patch B was only slightly greater than one third of the area of the other two patches.

Another aspect of sampling which adversely affected the patches was trampling and this factor is harder to quantify. Patch B was narrow and long and hence it was possible to avoid stepping into it while searching for whelks and sampling pneumatophores. In figure 13 it is apparent that pneumatophore death was much less in patch B than in the other patches. Similarly a comparison of figure 22 with figures 21 and 23 indicate that the elimination of B. amphitrite due to pneumatophore death was greatly reduced by the avoidance of trampling.

Pneumatophore death and the elimination of B. amphitrite by this factor was most pronounced in patch C which was fairly oval in shape and suffered much trampling in surveys. Patch A was convoluted in shape and a number of protruding "arms" could be walked around reducing trampling damage. Nevertheless both A and C were severely damaged during surveys. At the completion of the study there were areas which were bare of pneumatophores whereas at the commencement the pneumatophore coverage was homogeneous.

The three patches, D, E and F, being less frequently surveyed, remained fairly evenly covered and did not deteriorate. The marked deterioration of A and in particular C patch by June 1975 compared to the less surveyed patches led to the replanning of the survey techniques. Rather than completely destroy the patches, particularly as the predator feeding preferences following the expected spring B. amphitrite settlement were sought, the surveys were conducted less frequently. Declining barnacle density however, necessitated increasing the number of pneumatophores removed to about 50.

The cutting of pneumatophores may have encouraged their replacement although trampling may have prevented this from happening. These aspects could not be quantified. Pneumatophore death was not restricted to the older and larger pneumatophores as small new ones often shrivelled and died. This may also be due to trampling affecting the aerial root system.

Experimenter trampling, cutting of pneumatophores and disturbance of the surrounding mud may have led to the patches "ageing". Natural "ageing" of non-surveyed patches was indicated by a silting up of the shallow depressions in which they are located. Given the amount of disturbance of the mud around the surveyed patches an increased rate of silting up may be expected. Nevertheless this is a predominantly long term factor which should not greatly have affected this study.

TABLE 8 Number of pneumatophores and attached barnacles removed during sampling.

<u>Date</u>	<u>Patch A</u>			<u>Patch B</u>			<u>Patch C</u>		
	Pneumatophores	<u>B. amphitrite</u>	<u>E. modestus</u>	Pneumatophores	<u>B. amphitrite</u>	<u>E. modestus</u>	Pneumatophores	<u>B. amphitrite</u>	<u>E. modestus</u>
13/2/75	20	81	53	19	8	172	20	54	100
28/2/75	20	56	72	20	7	149	20	26	94
16/3/75	20	51	141	20	7	170	24	44	173
3/4/75	20	89	154	20	11	273	20	30	84
2/5/75	20	50	123	20	10	138	20	30	78
10/6/76	30	59	140	20	4	50	24	13	50
1/7/75	50	13	38	50	6	76	49	12	156
14/8/75	46	37	65	43	10	188	41	22	86
11/9/75	49	18	211	60	3	95	53	13	176
21/10/75	47	12	205	49	8	200	50	9	152
24/11/75	52	26	127	49	13	75	60	68	192
17/12/75	39	18	142	37	19	108	42	31	136
6/2/76	54	30	202	50	9	169	41	16	126
TOTAL:	467	403	1548	457	100	1542	464	288	1409
	Total from 16/3/75			Total from 16/3/75			Total from 16/3/75		

5.14 Pneumatophore dynamics

5.1.4.1. Methods

Pneumatophore death is a factor which leads to the elimination of barnacles. The extent to which it was responsible for eliminating B. amphitrite which settled in spring 1974 is calculated as follows. The period was divided into four sections, the first three being three months apart and the fourth at the end of the surveys. The total number of pneumatophores per square metre was estimated on each date as outlined in the sampling procedures and the percentage of these surviving from the last settlement period was estimated by determining the proportion which have either dead or living B. amphitrite on them. The number of pneumatophores removed from the total patch in each survey is given in Table 8 and it is possible to calculate the number removed from a square metre between each of the assessment points. This figure is then corrected for the presence of new pneumatophores by assuming that sampling is random and removes the same proportion of old and new.

As a result estimates of the percentage of pneumatophores surviving and the percentage removed during sampling are obtained. It can be assumed that the percentage required to account for those originally present is the portion which died between the dates shown.

5.1.4.2 Results

The percentage of pneumatophores surviving at different assessment points between 16/3/75 and 6/2/76 is estimated in Table 9. Mortality is lowest in patch B, only 7.5%, which indicates that the larger readings, 27.1% in A and 44.6% in C, over the year ~~were~~ probably due to experimenter trampling. The advantage which this conferred on B was annulled by the larger mortality figure due to sampling. A diagrammatic representation of the comparative extents of mortality from these two factors is shown in figure 13.

The mean length of pneumatophores is shown in figure 11 and is fairly constant throughout the entire period. A slight drop is apparent in June and corresponds to an increase in pneumatophore number shown in Figure 12

TABLE 9. Determination of the fate of pneumatophores which were present during the 1975 summer B. amphitrite settlement season.

<u>Patch A</u>	<u>16/3/75</u>	<u>10/6/75</u>	<u>11/9/75</u>	<u>6/2/76</u>
Pneumatophore density Number/metre ²	327	401	439	278
Percentage Old	100	57.9	63.1	75.9
Estimated number Old	327	232	277	211
Experimenter removed	60	126	187	
Olds removed (estimated)	34.7	79.5	141.9	
Conclusions				
Old surviving	100%	85.3%	84.7%	64.5%
Experimenter removed	-	2.0%	4.5%	8.4%
Died	-	12.7%	10.8%	27.1%
<u>Patch B</u>				
Pneumatophore density Number/metre ²	306	381	376	268
Percentage Old	100	65.9	72.6	75.8
Estimated number Old	306	251	273	204
Experimenter removed	60	113	195	
Olds removed (estimated)	39.5	82	147.8	
Conclusions				
Old surviving	100%	82%	89.2%	66.7%
Experimenter removed	-	5.6%	12.6%	25.8%
Died	-	12.4%	-	7.5%
<u>Patch C</u>				
Pneumatophore density Number/metre ²	315	365	360	184
Percentage Old	100	75.3	70	77.7
Estimated number Old	315	275	252	143
Experimenter removed	64	114	205	
Olds removed (estimated)	48.2	29.8	159.3	

TABLE 9 (cont)

Patch C	<u>16/3/75</u>	<u>10/6/75</u>	<u>11/9/75</u>	<u>6/2/76</u>
Conclusions:				
Old surviving	100%	87.3%	80%	45.6%
Experimenter removed	-	2.0%	5.0%	9.8%
Died	-	0.7%	15.0%	44.6%

Figure 11. Length of pneumatophores ($\pm$ S.E.) in patches
A,B and C between February 1975 and March 1976.

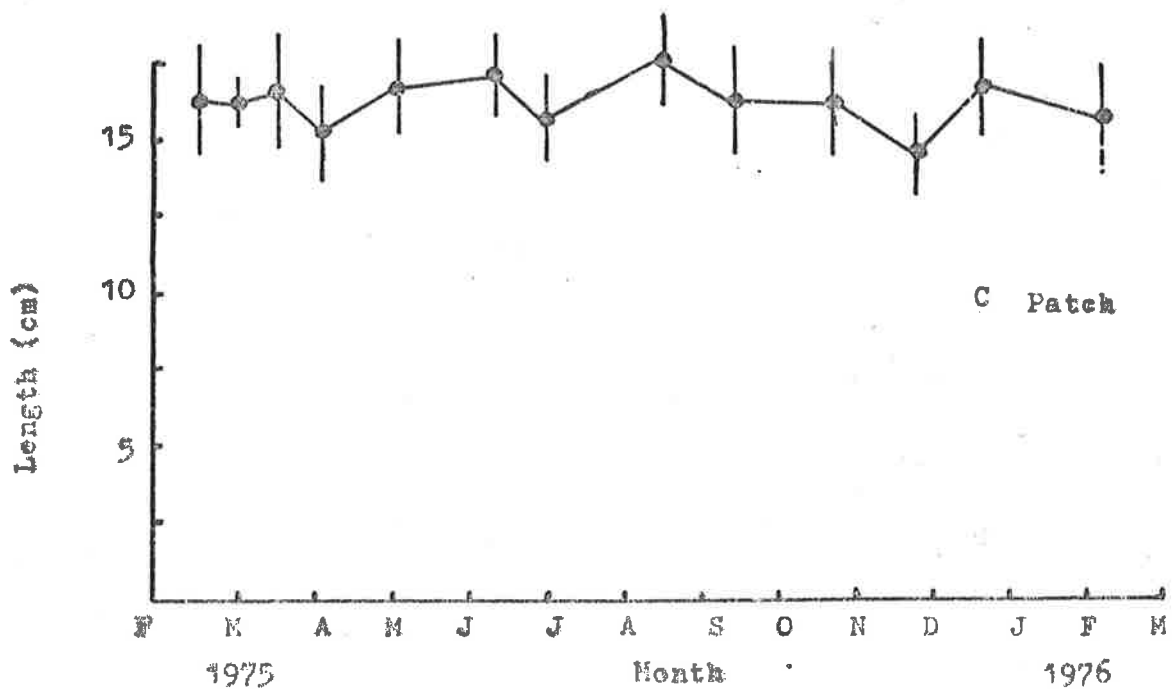
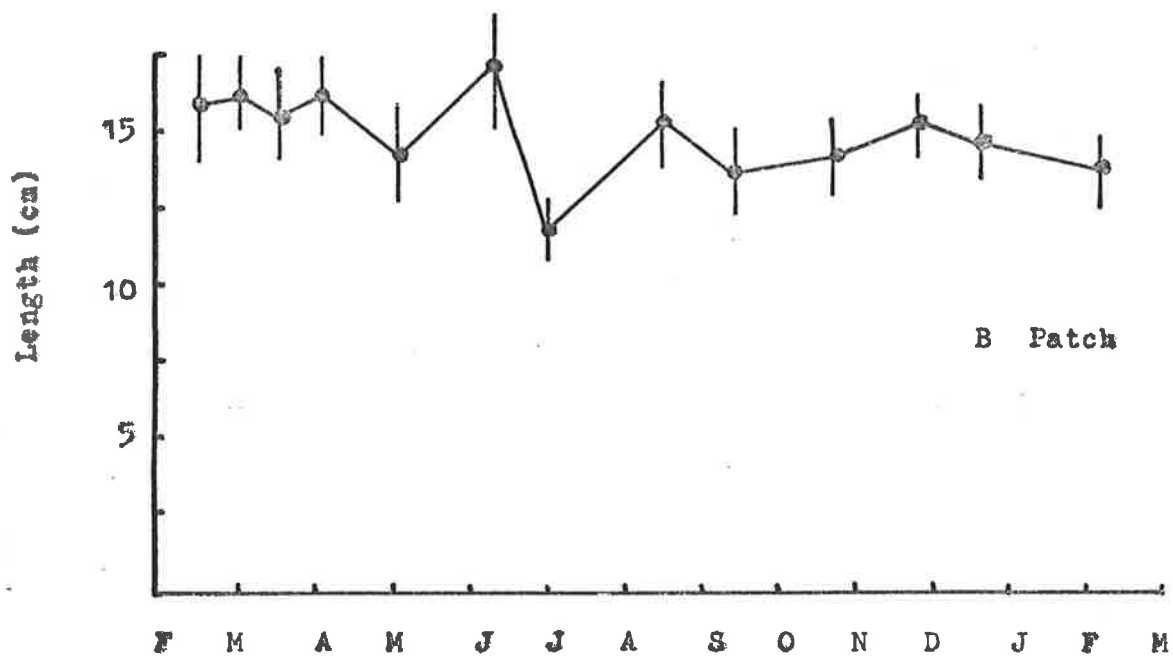
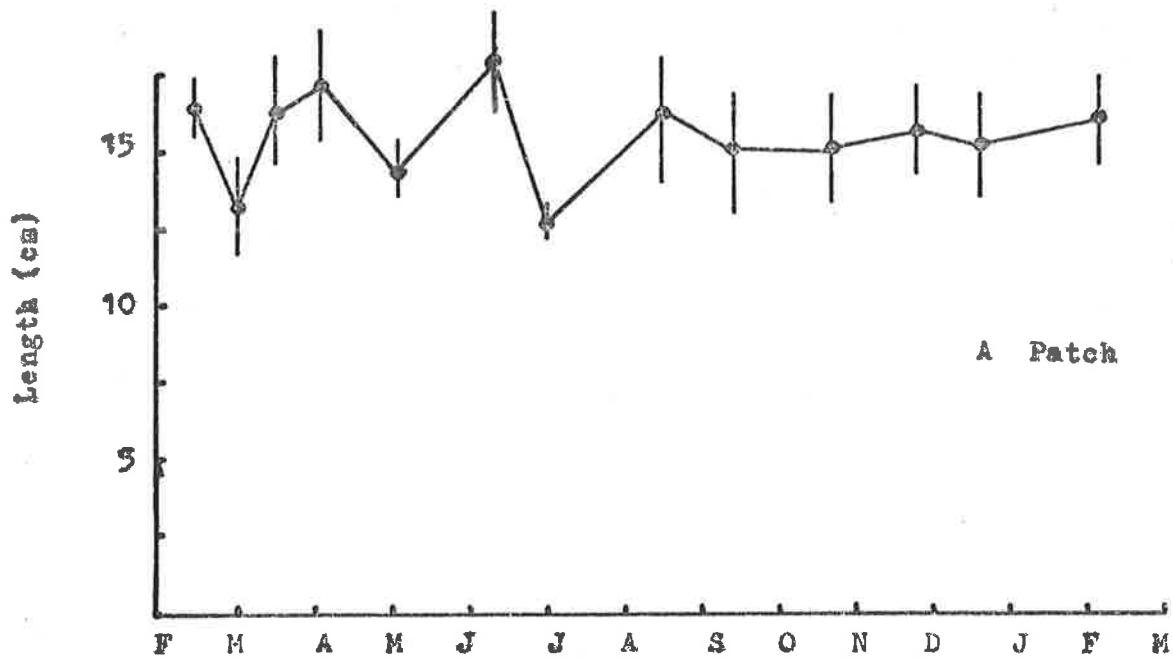
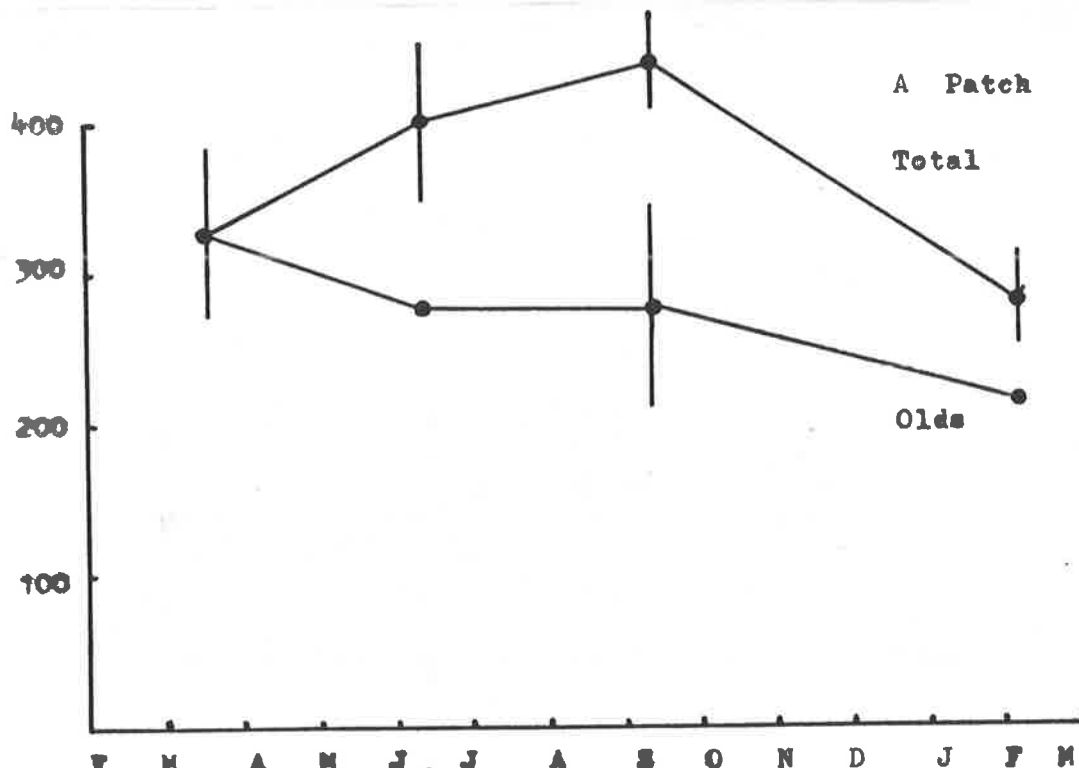
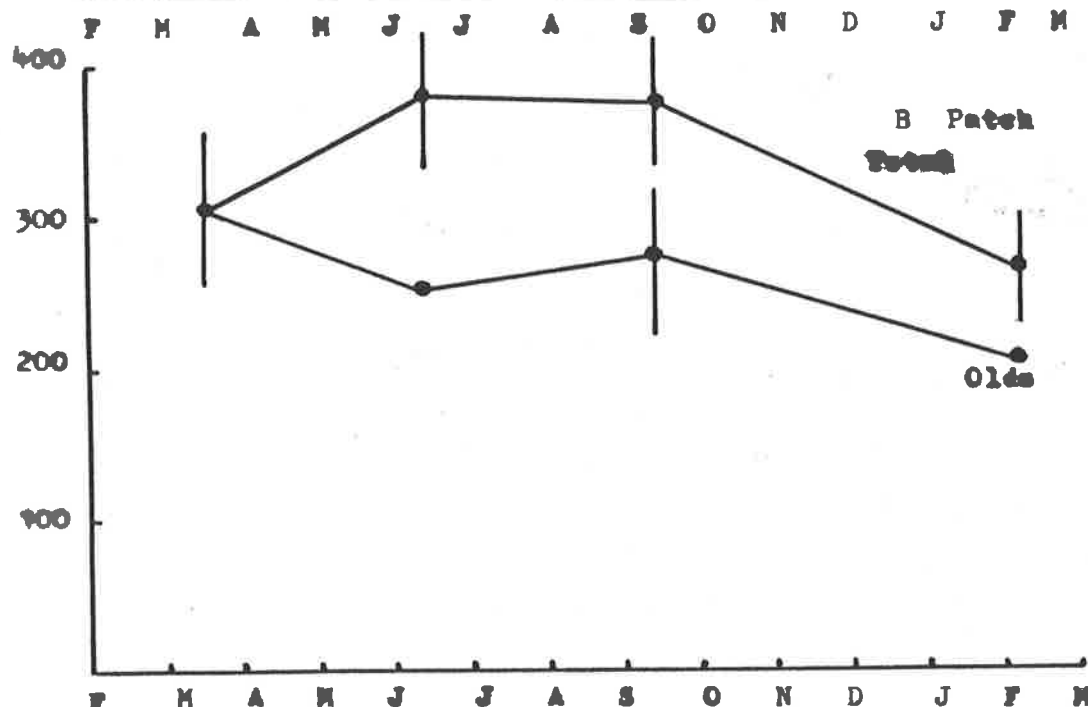


Figure 12. Number of pneumatophores per square metre ($\pm$ S.E.)
in patches A, B and C between February 1975 and February 1976.

Number



Number



Number

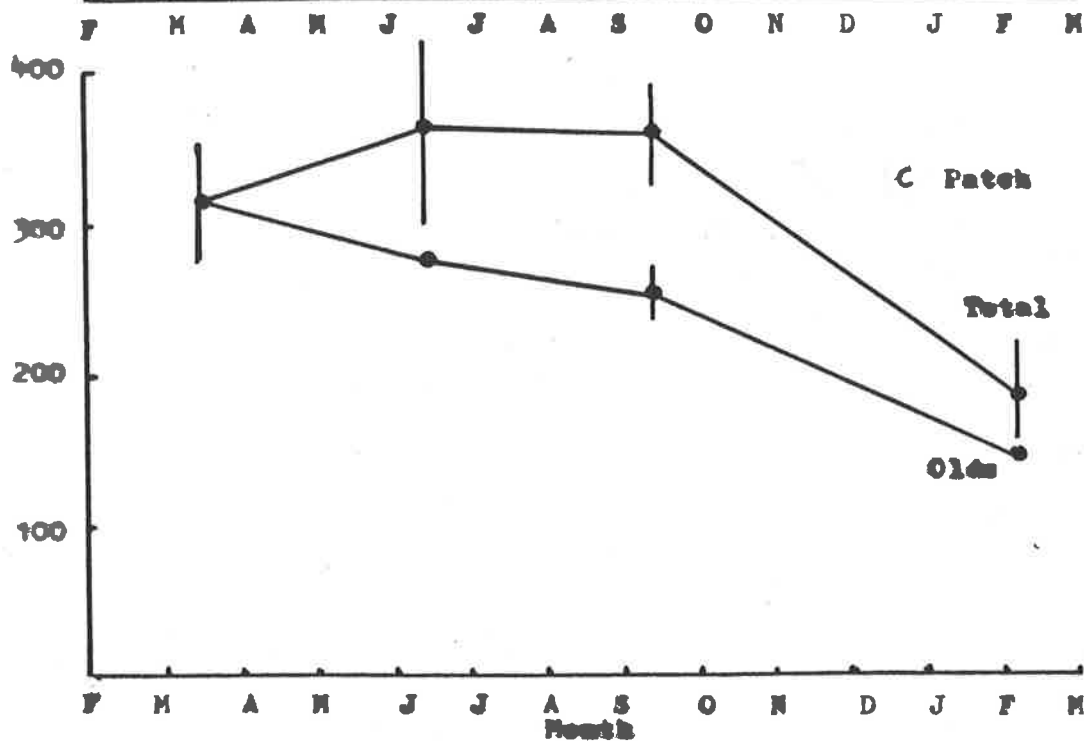


Figure 13. Survival of pneumatophores present in A,B and C patch between 16/3/75 (a) and 6/2/76 (d). The proportion of pneumatophores surviving to 10/6/75 (b), 11/9/75 (c), 6/2/76 (d) and the proportion which died or ^{have} been removed by the experimenter are shown.

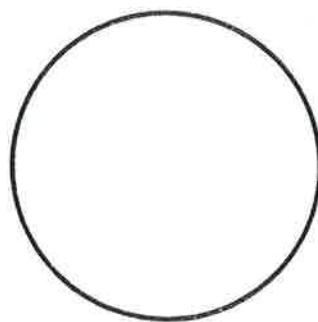
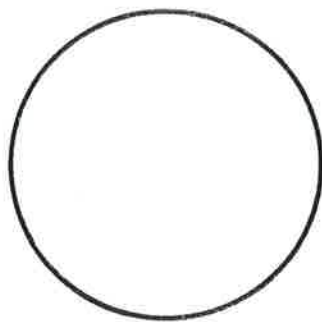
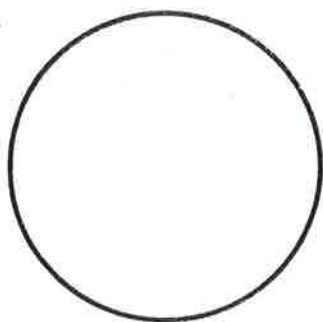
Key  Pneumatophores removed by experimenter

 Pneumatophores which died

A PATCH

B PATCH

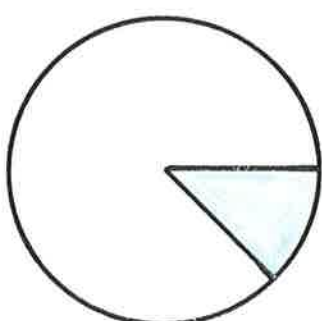
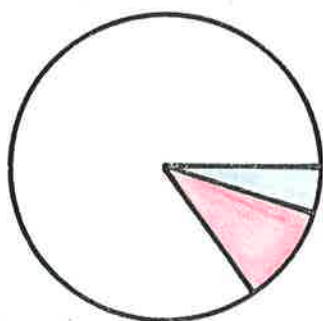
C PATCH



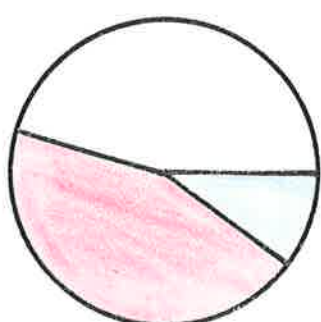
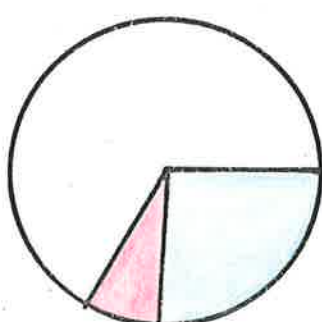
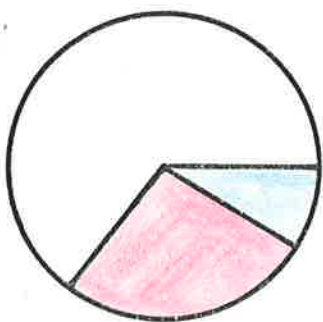
(a) 16/3/75



(b) 10/6/75



(c) 11/9/75



(d) 6/2/76

5.1.5.1 Introduction

The most accurate measure of barnacle density is the number of each species present per unit length of pneumatophore. It is also the most relevant measure as L. vinosa searches the pneumatophores for prey and is rarely found on the mud substratum in mangroves.

Density measures per unit area of a patch involve two further estimates, the number of pneumatophores per unit area and their mean length. This measure is however used to determine the longevity and causes of mortality of barnacle settlements. It would be difficult to use estimates in terms of unit length of pneumatophore in this case as the pneumatophores grow and die.

5.1.5.2. B. amphitrite density

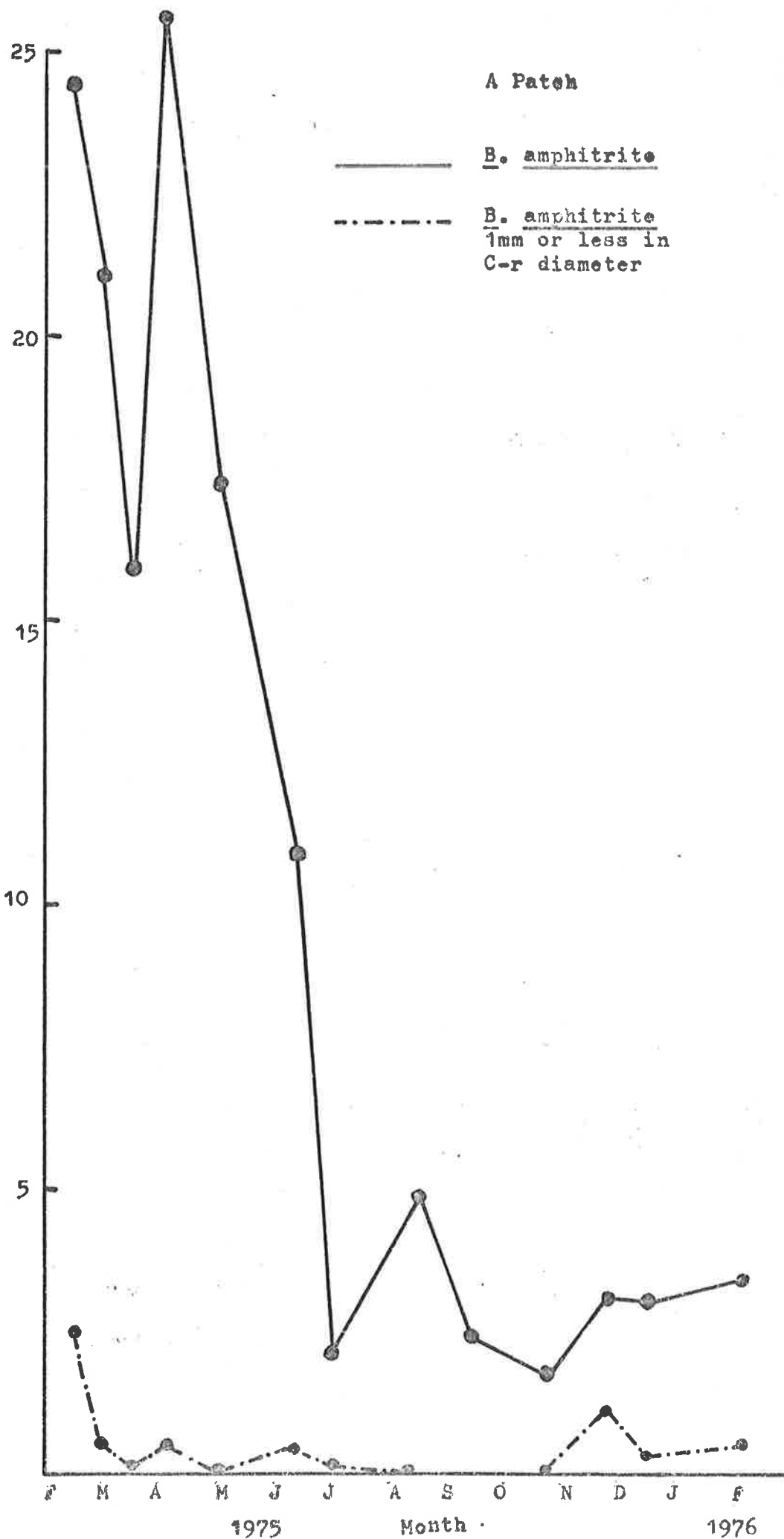
The number of B. amphitrite per unit length of pneumatophore in patches A, B and C are given in figures 14, 15 and 16. The density range in patch A is 1.7 to 25.6/metre, 3.5 to 0.7/metre in B, and 16.5 to 1.1/metre in C. Considerably higher densities were recorded in I patch, up to 170/metre, and in G patch, up to 80/metre. Aspects of interspecific and intraspecific competition which occur in these situations were not usually observed in A, B and C patches. Settlement is gregarious and on individual pneumatophores the density could be much higher than these patch average figures. Limited competition and hammock formation could take place, but was uncommon.

A sharp drop in density occurred in May and June in each patch and was particularly marked in A. Nevertheless the catastrophic mortality which eliminated all B. amphitrite in I patch did not take place. All other patches D, E, F, and G also showed marked declines in B. amphitrite density at this time. In the case of A and C a recovery to the previous density levels did not occur and in B although the density recovered it must be remembered that densities were never greater than 3.5/metre in the first case. The cause of the mortality in May and June is not known.

The slight spring settlement in 1975, compared to 1974, prevented

Figure 14. Density of B. amphitrite in A patch between
February 1975 and March 1976.

Number of B. amphitrite per metre length of pneumatophore



Number of B. amphitrite per metre length of pneumatophore

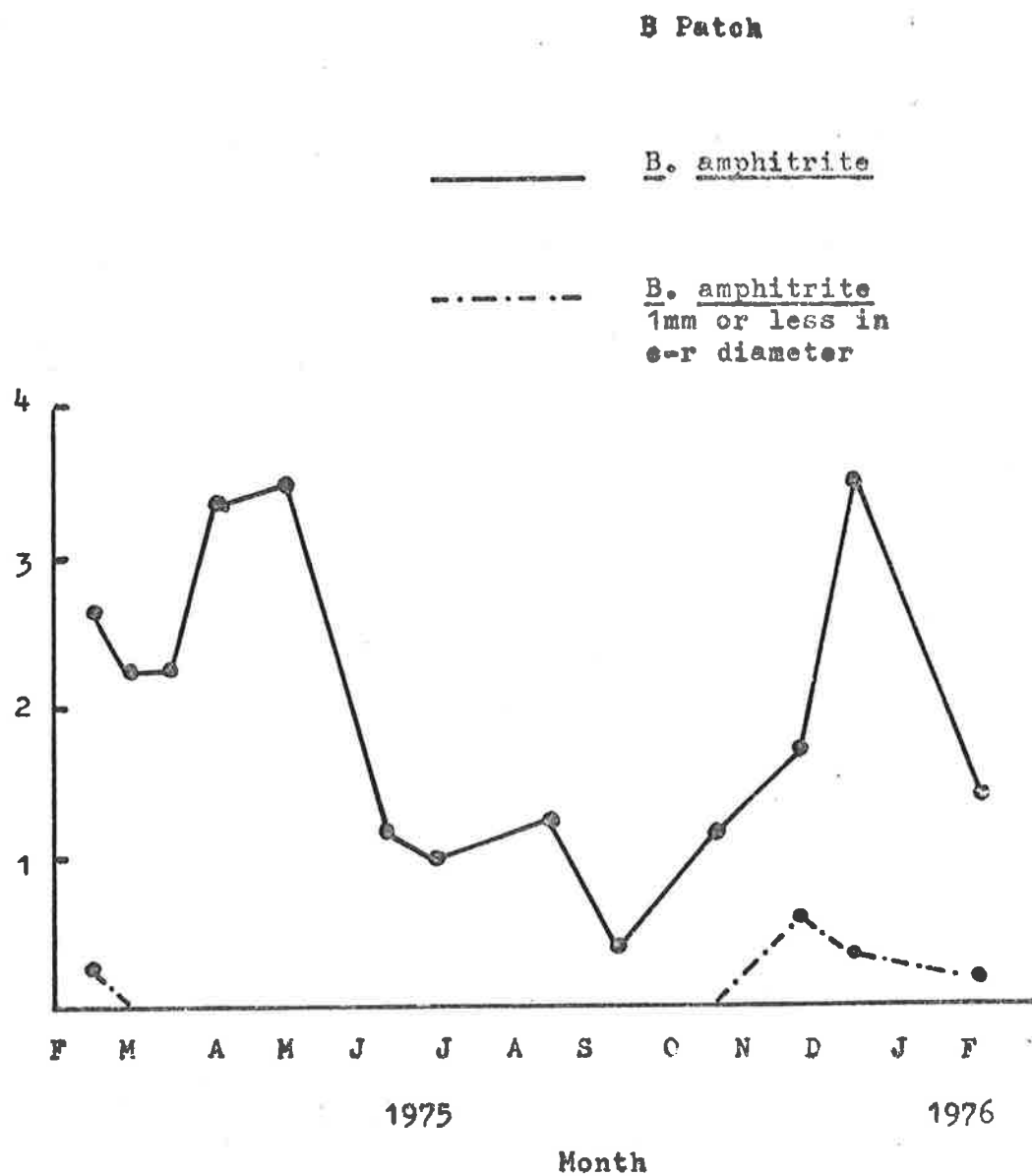


Figure 15. Density of B. amphitrite in B patch between February 1975 and March 1976.

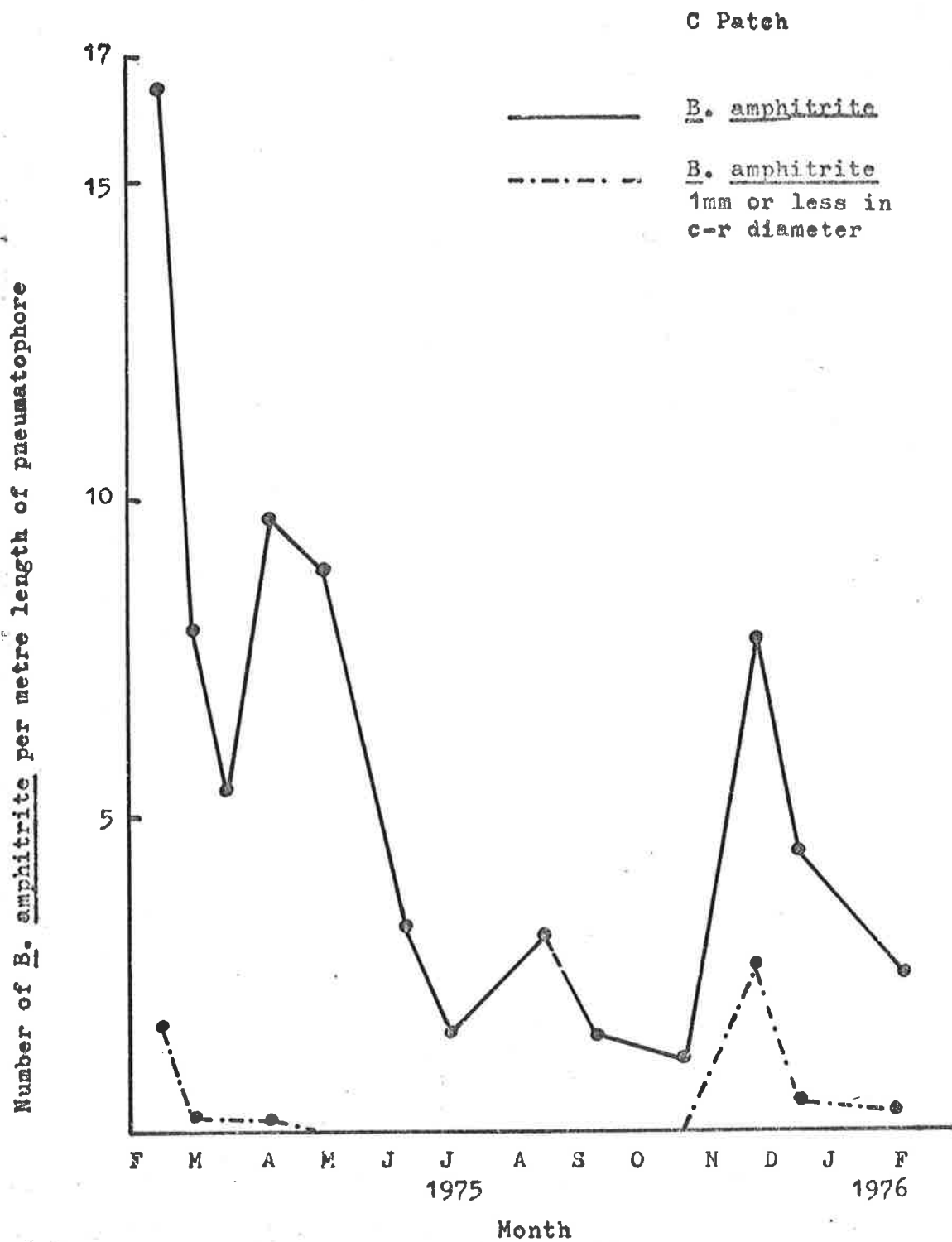


Figure 16. Density of B. amphitrite in C patch between February 1975 and March 1976.

the recurrence of high B. amphitrite densities. There is a rise in density in late March 1975 which does not appear to be related to settlement as few barnacles 1mm or less are present. The dead to living barnacle ratio shown in figure 20 does not decrease as would be expected following a settlement. The rise may be due to a sampling error.

5.1.5.3 E. modestus density

The density of E. modestus in A, B and C patches is shown in figures 17, 18 and 19. The ranges were 6.0 to 44.4/metre in A, 10.0 to 84.0/metre in B, and 12.0 to 30.5/metre in C. E. modestus was always more abundant than B. amphitrite.

Sharp drops in density occur in May and June indicating that the mortality observed in B. amphitrite at this time also occurred in E. modestus. Recovery due to heavy settlement took place in August and September. This settlement peak is the heaviest, but, not the only one which was observed during the study. Peaks are also apparent in February 1975 and 1976, October and to a lesser extent April. The result is somewhat sawtooth shape graphs indicating periodic waves of settlement.

5.1.5.4 Ratio of dead to living B. amphitrite

B. amphitrite mortality due to causes other than pneumatophore death results in an accumulation of dead B. amphitrite shells on the pneumatophores. Whelks drill through the opercular valves which are then dislodged and lost during inundation and as a result there is no method of determining if predation caused the death of a particular specimen. E. modestus is only attached to the substrate by a thin membrane and is usually detached from the substrate soon after death. Whelks often dislodge the fragile plates after consuming the barnacle. It is therefore not possible to gain any useful information from dead to living ratios for this species.

In the short term, particularly between successive readings, the dead to living ratio for B. amphitrite indicates whether death is exceeding recruitment. A large decrease in the ratio indicates

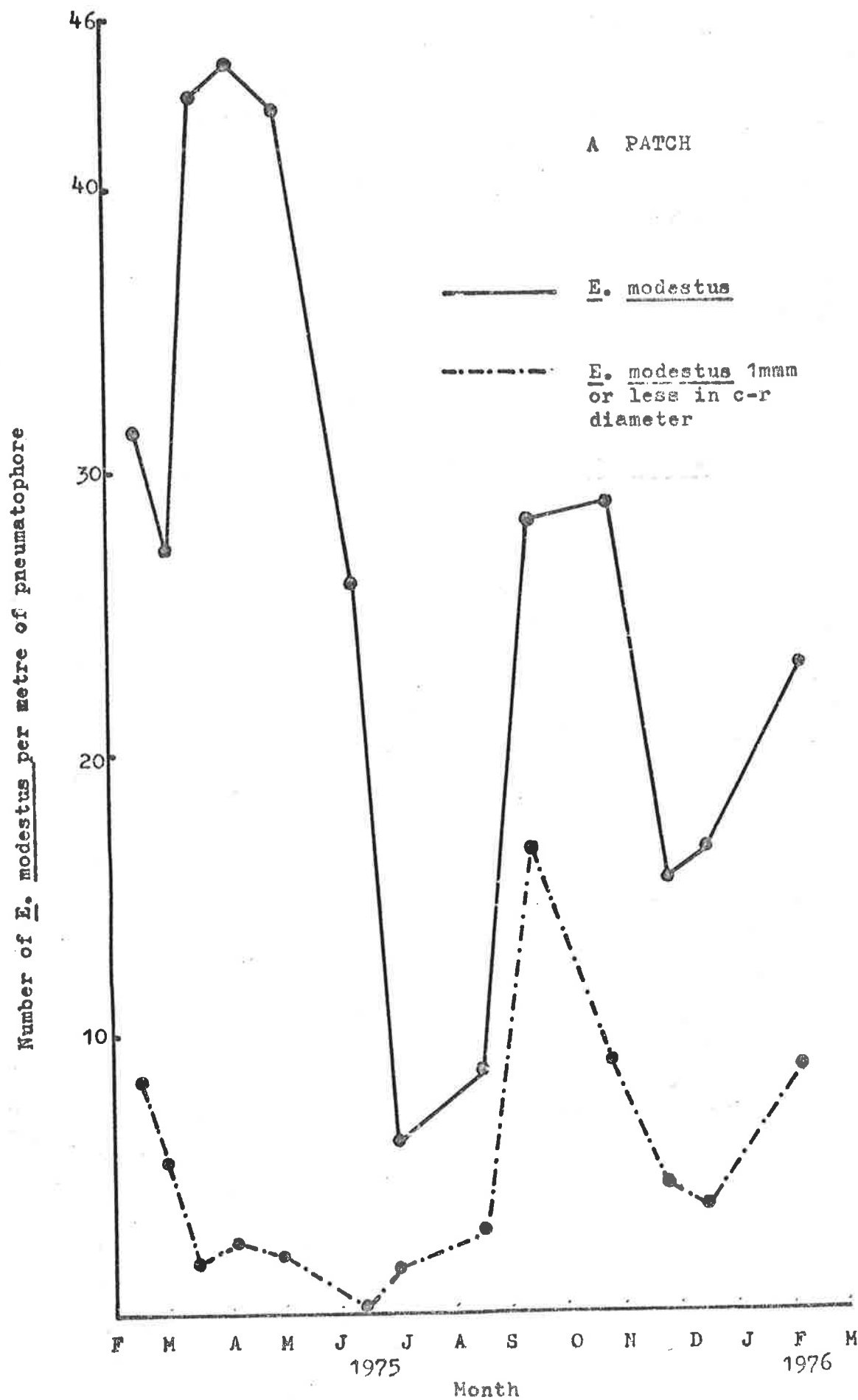


Figure 17. Density of E. modestus in A patch between February 1975 and March 1976.

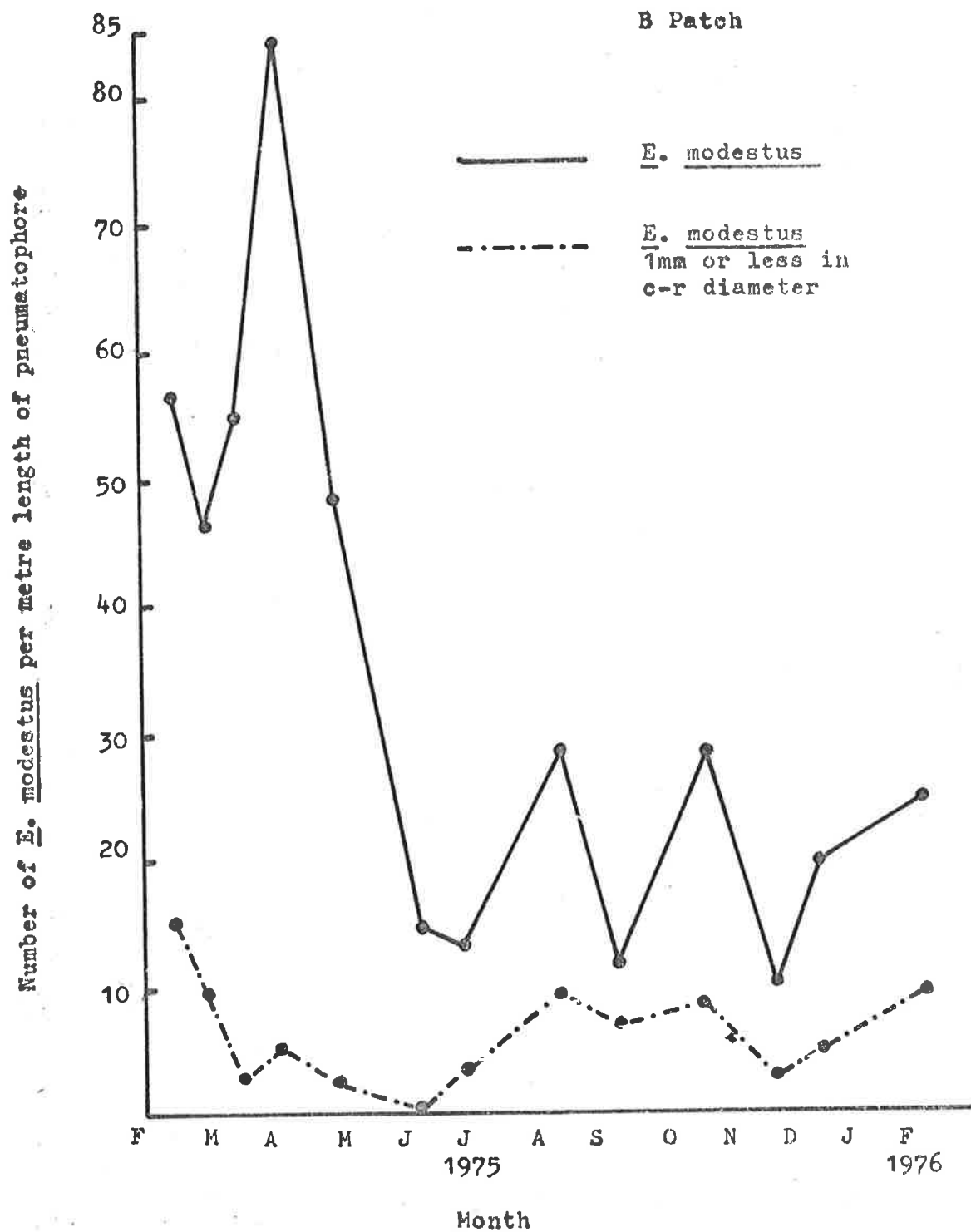


Figure 18. Density of E. modestus in B patch between February 1975 and March 1976.

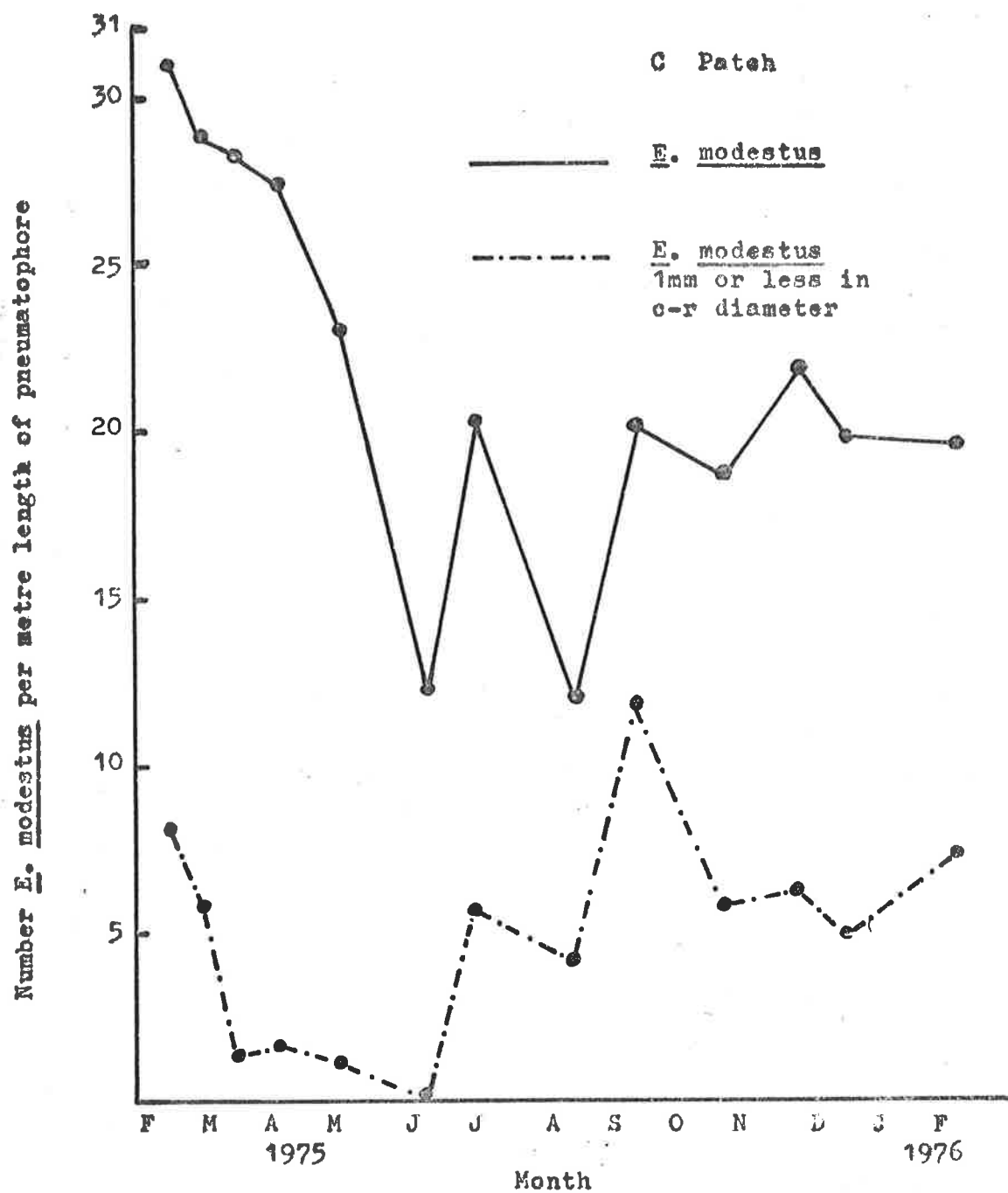


Figure 19. Density of E. modestus in C patch between February 1975 and March 1976.

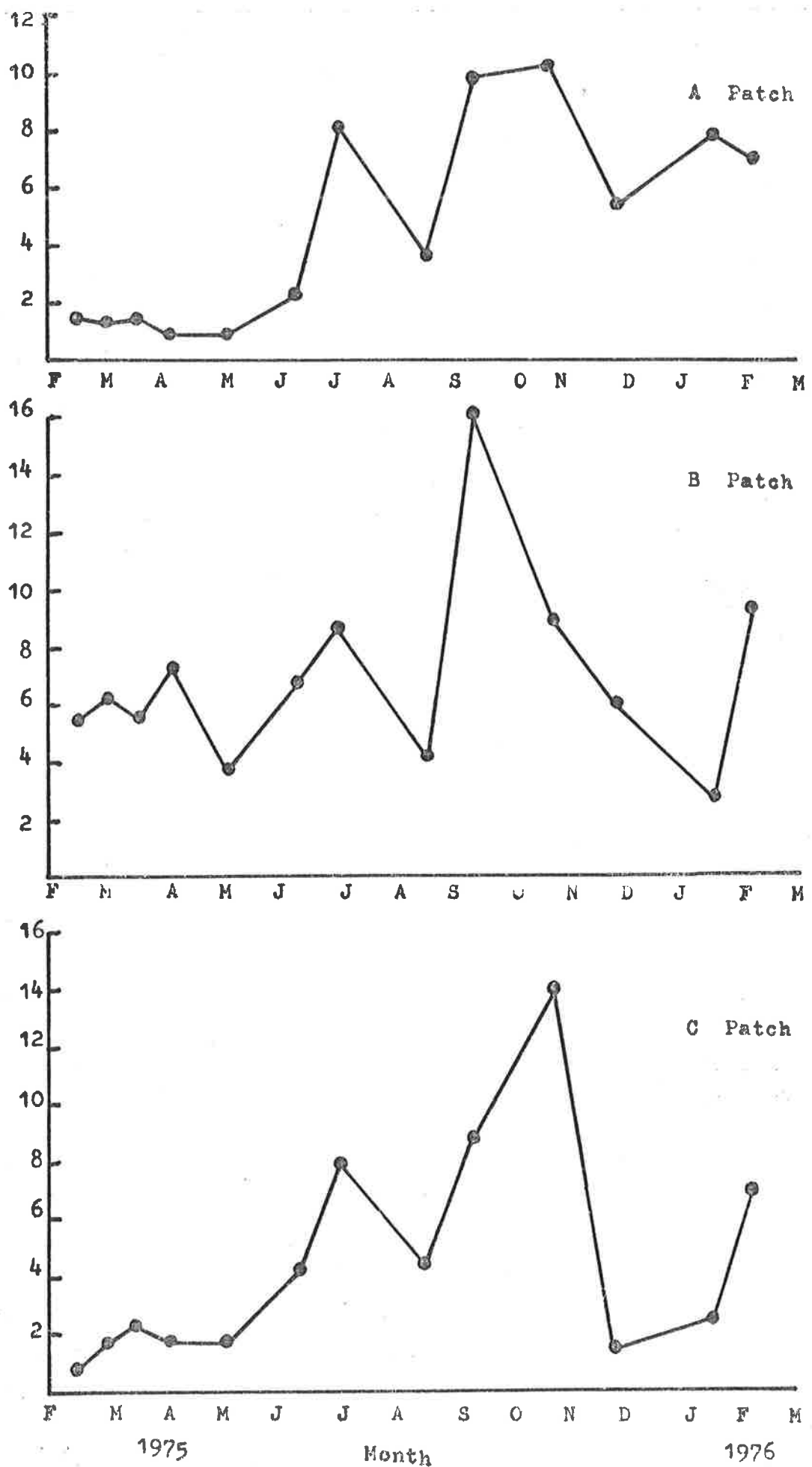


Figure 20. Ratio of dead to living B. amphitrite on pneumatophores

settlement, whereas large increases indicate heavy mortality. Barnacle shells are less stable on pneumatophores than on rock. Growth of the pneumatophore and death of the tissue immediately under a dead barnacle shell can result in the normally strongly cemented shells dislodging.

The dead to living B. amphitrite ratios are plotted in graphs in figure 20. The peak in June in each patch is related to the mortality which occurred at this time. A second peak in September and October would be due to increasing mortality since the last settlement period. The drop between these two peaks is possibly caused by the death of old pneumatophores which had been present at settlement periods before the most recent. These pneumatophores would have had an unusually high number of dead barnacles which would be removed from the estimate. In figure 12 there is a reduction in the number of old pneumatophores between March and September. The second drop in October and November is larger and due to the spring B. amphitrite settlement.

5.1.5.5. Effect of L. vinosa predation on B. amphitrite survival.

The number of barnacles which are consumed by L. vinosa in a given time interval can be estimated by the following formula.

Number of barnacles consumed /m² = Number of L. vinosa/m² X Number of barnacles eaten/L. vinosa/week X Number of weeks.

The average feeding rate of L. vinosa is 1.65 barnacles/week (section 9.3.8). The other factors vary according to patch and period under consideration and are listed in table 10.

Not all the barnacles which are consumed are B. amphitrite. The percentage of L. vinosa attacking B. amphitrite was calculated from the number of L. vinosa observed feeding on this species and the total number of L. vinosa feeding on both barnacle species during the given periods.

Percentage mortality in the B. amphitrite population due to L. vinosa predation could be calculated as the number of B. amphitrite/m² which were present on 16/3/75 and successive dates were known. The percentage mortality attributed to L. vinosa predation is included in figures

21,22 and 23.

TABLE 10 Percentage mortality attributed to L. vinosa on the B. amphitrite population which settled prior to 16/3/75.

(a) <u>Patch A</u>	<u>Period under consideration</u>		
	<u>to: 10/6/75</u>	<u>to: 11/9/75</u>	<u>to: 6/2/76</u>
Average number <u>L. vinosa</u> /m ²	7.2(⁺ 0.4 SE)	6.6(⁺ 0.6 SE)	4.2(⁺ 0.5 SE)
Number of weeks	12.3	13.3	21.1
Barnacles eaten/ <u>L. vinosa</u> /week	1.65	1.65	1.65
Number of barnacles consumed	146	145	146
<u>L. vinosa</u> attacking <u>B. amphitrite</u>	27%	20.7%	17.3%
Number of <u>B. amphitrite</u> eaten	39	30	12*
Mortality attributed to <u>L.</u>			
<u>vinosa</u> since 16/3/75	4.6%	8.1%	9.5%
Mortality between successive dates	4.6%	3.7%	7.4%
(b) <u>Patch B</u>			
Average number <u>L. vinosa</u> /m ²	10.1(⁺ 2.2 SE)	12.8(⁺ 1.6 SE)	12.1(⁺ 2.1 SE)
Number of weeks	12.3	13.3	21.1
Barnacles eaten/ <u>L. vinosa</u> /week	1.65	1.65	1.65
Number of barnacles consumed	205	281	421
<u>L. vinosa</u> attacking <u>B. amphitrite</u>	2.2%	6.1%	11.0%
Number of <u>B. amphitrite</u> eaten	5	17	11*
Mortality attributed to <u>L. vinosa</u>			
since 16/3/75	4.7%	20.6%	30.8%
Mortality between successive dates	4.7%	22.4%	57.9%
(c) <u>Patch C</u>			
Average number <u>L. vinosa</u> /m ²	6.1(⁺ 0.1 SE)	5.5(⁺ 0.6 SE)	4.3(⁺ 0.6 SE)
Number of weeks	12.3	13.3	21.1
Barnacles eaten/ <u>L. vinosa</u> /week	1.65	1.65	1.65

Table 10 Patch C (cont)

Number of barnacles consumed	124	121	150
<u>L. vinosa</u> attacking <u>B. amphitrite</u>	20.6%	18.7%	34.3%
Number of <u>B. amphitrite</u> eaten	26	23	23*
Mortality attributed to <u>L. vinosa</u> since 16/3/75	9.2%	17.3%	25.4%
Mortality between successive dates	9.2%	11.7%	25.6%

*This figure is corrected to take into account new settlement from November 1975. L. vinosa are assumed to attack new and old barnacles at random. A is therefore 48.4% of 25=12, B is 22.9% of 46=11 and C is 44.4% of 51=23.

5.1.5.6 Potential L. vinosa predation rate on B. amphitrite

The effect of L. vinosa predation on B. amphitrite, given in Table 10, was estimated taking into consideration the relative proportion of L. vinosa observed attacking this species. In Table 11, the possible effect of L. vinosa predation on B. amphitrite which settled prior to 16/3/75 if all L. vinosa attacked only this species is estimated.

TABLE 11. The maximum potential predation on B. amphitrite by L. vinosa if only this species of barnacle was consumed.

<u>PATCH</u>	<u>DATE</u>		
	<u>11/6/75</u>	<u>11/9/75</u>	<u>6/2/76</u>
A Maximum potential mortality	17.2%	34.2%	51.4%
B Maximum potential mortality	191.6%	454.2%	847.7%
C Maximum potential mortality	43.7%	86.3%	139.1%

These potential mortalities are included in figures 21, 22 and 23.

On the basis of these estimates it can be concluded that B. amphitrite would be eliminated from patch B by 10/6/75 and patches A and C by 11/9/75 if other forms of mortality are included. The survival of B. amphitrite until the following breeding season is therefore dependent on L. vinosa not concentrating its attacks upon its preferred prey species.

5.1.5.7 Effect of L. vinosa predation on E. modestus

L. vinosa concentrates most of its attacks on the numerically more abundant E. modestus although this is the less preferred prey in choice experiments. The maximum predator consumption of barnacles, Table 10, is not sufficient to eliminate E. modestus even if attacks were confined to this species. Periodic restocking of the patches by E. modestus settlements maintains a fairly high density of barnacles. Outside of the 16/3/75 to 10/6/75 period E. modestus settled at nearly two-month intervals in sufficient numbers to prevent serious depletion by predation. The settlement rates of E. modestus are included in Table 12.

5.1.5.8 Barnacle settlement from 16/3/75 to 6/2/76

An estimate of the number of barnacles settling/m² of patch can be obtained by assuming that the number of barnacles 1mm or less in carino-rostral diameter in each month is due to new settlement. Size frequency histograms for B. amphitrite and E. modestus are shown in figures 6 and 7.

There are problems with this simple estimation procedure as small barnacles could be those from an earlier settlement which failed to grow. The small percentage of B. amphitrite 1mm in carino-rostral diameter recorded before 11/9/75 have been ignored as very small individuals were not also found. Examination of the gonads, reported in section 3.3, indicated that larvae were not being released. No very small E. modestus were found before 16/7/75 and the few individuals 1mm in carino-rostral diameter present before this date were similarly ignored in Table 12. A second cause of error in this estimation procedure could arise if some

barnacles grow to more than 1mm in carino-rostral diameter in one month.

In Table 12 the number of barnacles settling in each patch is shown.

TABLE 12 Estimated number of barnacles settling per square metre of patch

<u>Patch</u>	<u>Species</u>	<u>Period</u>		
		16/3/75 to 10/6/75	10/6/75 to 11/9/75	11/9/75 to 6/2/76
A	<u>B. amphitrite</u>	-	-	77
	<u>E. modestus</u>	-	2287	2618
B	<u>B. amphitrite</u>	-	-	36
	<u>E. modestus</u>	-	718	1234
C	<u>B. amphitrite</u>	-	-	71
	<u>E. modestus</u>	-	1445	782

5.1.5.9 Survival of B. amphitrite which settled prior to 16/3/75

The number of B. amphitrite which survive until 10/6/75 and 11/9/75 in the patches A, B and C is equal to the number of living B. amphitrite as no new settlements occurred before 11/9/75. Some settlement did take place between 11/9/75 and 6/2/76 and this complicates the assessment of the number of B. amphitrite surviving in the patches since 16/3/75.

The number of barnacles settling between 11/9/75 and 6/2/76 was calculated in section 5.1.5.8. In Table 13(a) the number of these barnacles which are mixed with survivors from settlements prior to 16/3/75 is determined. To make this estimate random settlement on both new and old pneumatophores is assumed. The number which settle on old pneumatophores is calculated and to assess the number which survive until 16/2/75 two corrections are made. These corrections are for pneumatophore death and removal by the experimenter.

The total number of B. amphitrite on old pneumatophores is given in Table 13(b). The number of these barnacles which settled prior to 16/3/75 is determined by subtracting the estimated number of new settlers present.

The proportion of B. amphitrite surviving until the spring 1975 breeding season was 19.1% in A patch, 17.8% in B patch and 31.7% in C patch. Barnacles produce large numbers of larvae and these survivors have the potential to restock the patches.

TABLE 13 Determination of the number of B. amphitrite which settled prior to 16/3/75 living until 6/2/76.

(a) Determination of number of B. amphitrite settling on old pneumatophores between 11/9/75 and 6/2/76.

	<u>A</u>	<u>B</u>	<u>C</u>
Number of <u>B. amphitrite</u> settling/m ²	77	36	71
Number of pneumatophores/m ²	278	268	184
Number of old pneumatophores/m ²	211	204	143
Number of <u>B. amphitrite</u> settling on old pneumatophores	58	27	55
Number removed by pneumatophore death	10	2	16
Number removed by experimenter	2	3	3
∴ Number remaining	46	22	34

(b) Number of B. amphitrite surviving from 16/3/75

	<u>A</u>	<u>B</u>	<u>C</u>
Number of <u>B. amphitrite</u> on old pneumatophores	116	36	56
Estimated number of new settlers	46	22	34
∴ Number of survivors from 16/3/75	70	14	22

5.1.6.0 Relative importance of factors causing mortality in the B. amphitrite population

The major factors causing mortality in B. amphitrite over the period 16/3/75 to 6/2/76 are summarised in Table 14. Estimates of the influence of these factors between 10/6/75 and 6/2/76 and also the period 11/9/75

to 6/2/76 are shown in Tables 15 and 16. Diagrammatic representations are shown in figures 21 to 23.

The barnacles accounted for under the heading "other causes of mortality" are those which were eliminated from the population by factors other than predation by L. vinosa, death of pneumatophores and experimenter removal. There is a sharp rise in the number of barnacles in this category between 10/6/75 and 11/9/75. This corresponds to the heavy mortality in June which was indicated by the decrease in the density of living B. amphitrite (section 5.1.5.2) and the rise in the ratio of dead to living barnacles (section 5.1.5.4).

TABLE 14 Causes of mortality in the B. amphitrite population which settled prior to 16/3/75 in the period 16/3/75 to 6/2/76.

<u>Patch A</u>	<u>10/6/75</u>	<u>11/9/75</u>	<u>6/2/76</u>
Pneumatophore death	12.7%	10.8%	27.1%
Experimenter removal	2.0%	4.5%	8.4%
<u>L. vinosa</u> predation	4.6%	8.1%	9.5%
Percentage surviving	94.4%	19.1%	8.7%
Other causes of mortality	-	65.6%	55.8%

<u>Patch B</u>			
Pneumatophore death	12.4%	0	7.5%
Experimenter removal	5.6%	12.6%	25.8%
<u>L. vinosa</u> predation	4.7%	20.6%	30.8%
Percentage surviving	71.0%	17.8%	10.3%
Other causes of mortality	11.0%	69.6%	56.4%

<u>Patch C</u>	<u>10/6/75</u>	<u>11/9/75</u>	<u>6/2/76</u>
Pneumatophore death	0.7%	15.0%	44.6%
Experimenter removal	2.0%	5.0%	9.8%
<u>L. vinosa</u> predation	9.2%	17.3%	25.4%
Percentage surviving	69.4%	31.7%	7.75%
Other causes of mortality	27.9%	48.3%	37.9%

TABLE 15 Causes of mortality in the B. amphitrite population which settles prior to 16/3/75 in the period 10/6/75 to 6/2/76.

<u>Patch A</u>	<u>11/9/75</u>	<u>6/2/76</u>
Pneumatophore death	-	16.3%
Experimenter removal	2.5%	6.4%
<u>L. vinosa</u> predation	3.7%	5.2%
Percentage surviving	20.2%	9.2%
Other causes of mortality	73.6%	62.9%

<u>Patch B</u>		
Pneumatophore death	-	-
Experimenter removal	7.0%	20.2%
<u>L. vinosa</u> predation	22.4%	36.8%
Percentage surviving	25.0%	14.5%
Other causes of mortality	45.6%	28.5%

<u>Patch C</u>		
Pneumatophore death	14.3%	43.9%
Experimenter removal	3.0%	7.8%
<u>L. vinosa</u> predation	11.7%	23.4%
Percentage surviving	45.7%	11.2%
Other causes of mortality	25.3%	13.7%

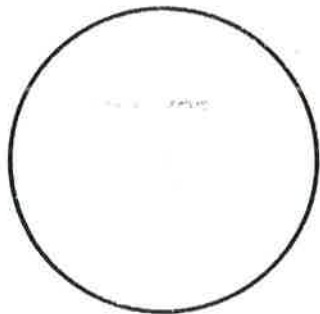
Figure 21. Survival of B. amphitrite in A patch. The proportion of B. amphitrite surviving and the proportion eliminated by different factors between the dates 16/3/75(a), 10/6/75(b), 11/9/75(c) and 6/2/76(d) are shown. The maximum potential mortality which would occur if L. vinosa concentrated its attacks on this species is also indicated.

KEY

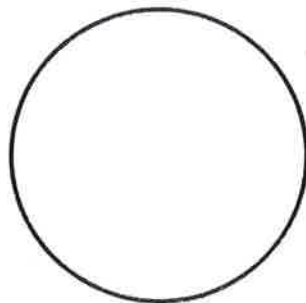
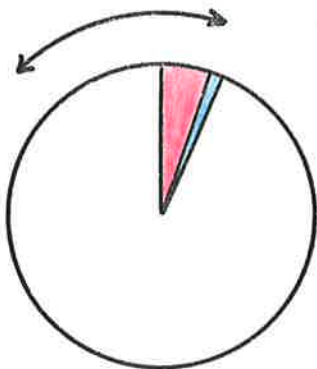
-  Death due to L. vinosa
-  Removed by experimenter
-  Eliminated by pneumatophore death
-  Other causes of mortality
-  Maximum potential mortality which could be caused by L. vinosa

(a) 16/3/75

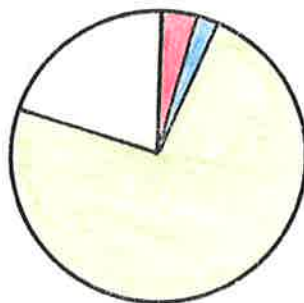
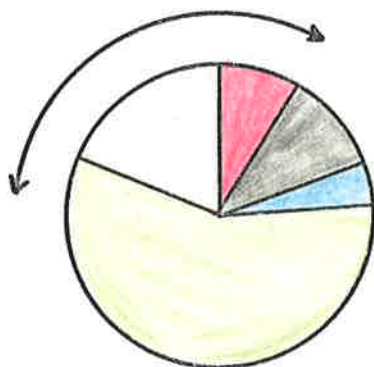
A PATCH



(b) 10/6/75



(c) 11/9/75



(d) 6/2/76

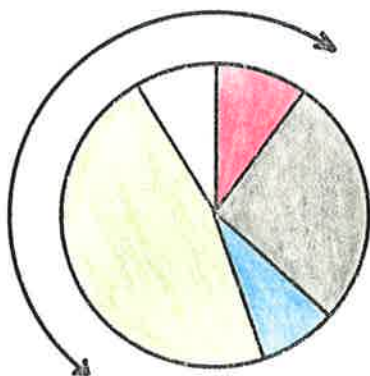


Figure 22. Survival of B. amphitrite in B patch. The proportion of B. amphitrite surviving and the proportion eliminated by different factors between the dates 16/3/75(a), 10/6/75(b), 11/9/75(c) and 6/2/76(d) are shown. The maximum potential mortality which would occur if L. vinosa concentrated its attacks on this species is also indicated.

KEY



Death due to L. vinosa



Removed by experimenter



Eliminated by pneumatophore death



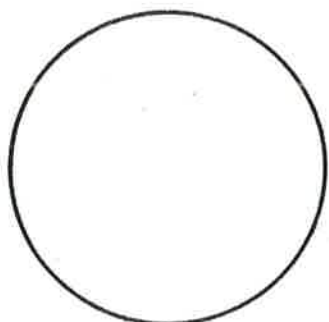
Other causes of mortality



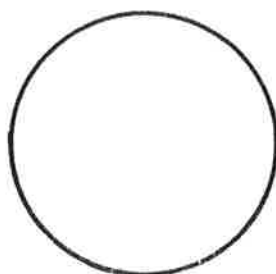
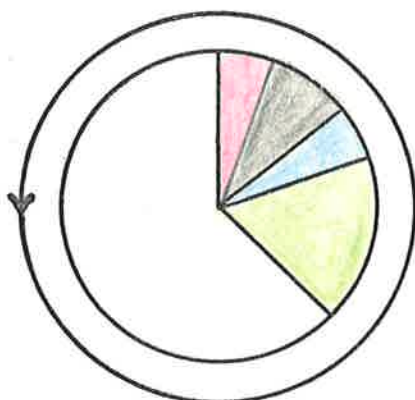
Maximum potential mortality which could be caused by L. vinosa

(a) 16/3/75

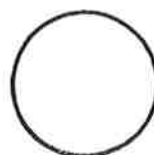
B PATCH



(b) 10/6/75



(c) 11/9/75



(d) 6/2/76



Figure 23. Survival of B. amphitrite in C patch. The proportion of B. amphitrite surviving and the proportion eliminated by different factors between the dates 16/3/75(a), 10/6/75(b), 11/9/75(c) and 6/2/76(d) are shown. The maximum potential mortality which would occur if L. vinosa concentrated its attacks on this species is also indicated.

KEY



Death due to L. vinosa



Removed by experimenter



Eliminated by pneumatophore death



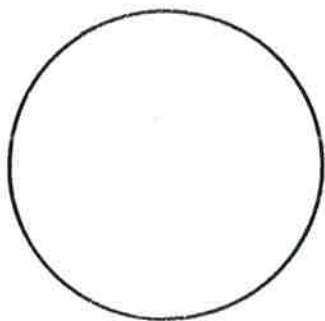
Other causes



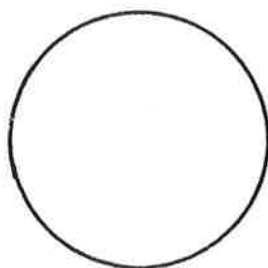
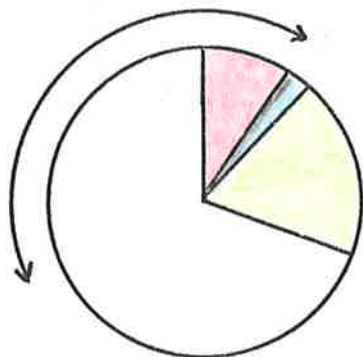
Maximum potential mortality which could be caused by L. vinosa

(a) 16/3/75

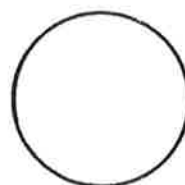
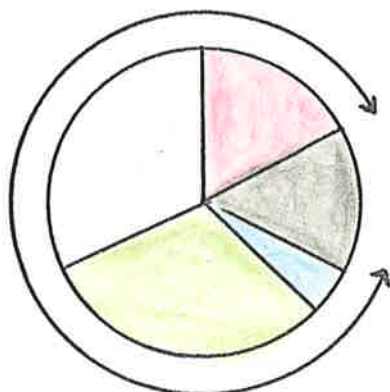
C PATCH



(b) 10/6/75



(c) 11/9/75



(d) 6/2/76

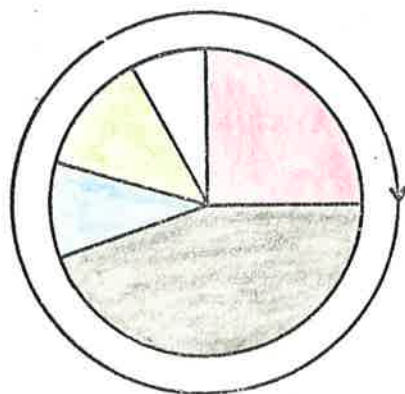


TABLE 16 Causes of mortality in the B. amphitrite population which settled prior to 16/3/75 in the period 11/9/75 to 6/2/76.

	<u>Patch</u>		
	<u>A.</u>	<u>B.</u>	<u>C.</u>
Pneumatophore death	16.3%	7.5%	29.6%
Experimenter removal	3.9%	13.2%	4.8%
<u>L. vinosa</u> predation	16.2%	21.4%	25.5%
Percentage surviving	45.7%	57.9%	24.4%
Other causes of mortality	17.9%	-	15.7%

5.2 Dynamics of barnacle populations on a small island, subject to L. vinosa and B. paivae predation.

5.2.1 Introduction

A small island, located approximately twenty metres off Garden Island, received a series of extremely heavy barnacle settlements in spring 1974 and summer 1975. The feeding behaviour of the L. vinosa population and the dynamics of the barnacles was investigated on this island. This atypical foraging area for L. vinosa was chosen for examination as little was known about the probable fate of prey in the typical foraging patches. It was considered possible that these patches would be quickly eliminated and no long term data would be obtained. The island had an initial barnacle population of in excess of 7,000/m² and this was considered adequate for many years of L. vinosa predation. These initial impressions proved incorrect but, nevertheless interesting results on prey selection at high barnacle densities were obtained and the fates of the barnacle populations were ascertained.

5.2.2 Characteristics unique to I patch

The central flat area of the small island was designated as I patch. The island was 25.5 metres in length and 10.4 metres at its widest. The

central area was thickly covered with unusually small pneumatophores which never averaged more than 12.3cm in length in any survey. Unlike the inland patches this patch was subject to sufficiently heavy barnacle settlement to nearly completely cover all available pneumatophores. The island is slightly lower in the intertidal zone than the other mangroves and B. paivae can swarm onto it from the surrounding mud flats.

5.2.3 Gastropod predation

Two gastropod predators, L. vinosa and B. paivae, are found on the island. They are both capable of drilling B. amphitrite and E. modestus. Predation on E. modestus was however rarely observed. The population density of the two predators is shown in figure 24. L. vinosa was fairly constant in abundance, at just under $3/m^2$, for most of the period of the study.

In contrast the density of B. paivae varied markedly. At the commencement of the study there were only $0.3/m^2$ and the density rose sharply to a maximum of $56/m^2$ in February 1975 and then declined to $3/m^2$. This decline is almost certainly related to the elimination of the barnacle population in June. The shape of the B. paivae density graph in figure 24 and the shape of the graph of the ratio of living to dead B. amphitrite shown in figure 27 are similar although there is a time lag.

B. paivae, unlike L. vinosa, aggregate when feeding and up to 24 have been observed on a long pneumatophore. Rarely more than two L. vinosa are found on one pneumatophore irrespective of the number of barnacles present. B. paivae swarmed onto the island in response to the rich food source. The mortality of most of the barnacles in June destroyed the food source and most of the B. paivae returned to the mud flats to attack its previous prey, that is various bivalves particularly Venerupis crebrelamellata and Modiolus inconstans.

B. paivae has been observed attacking L. vinosa in the field. An examination of 200 L. vinosa indicated that 4% had been attacked.

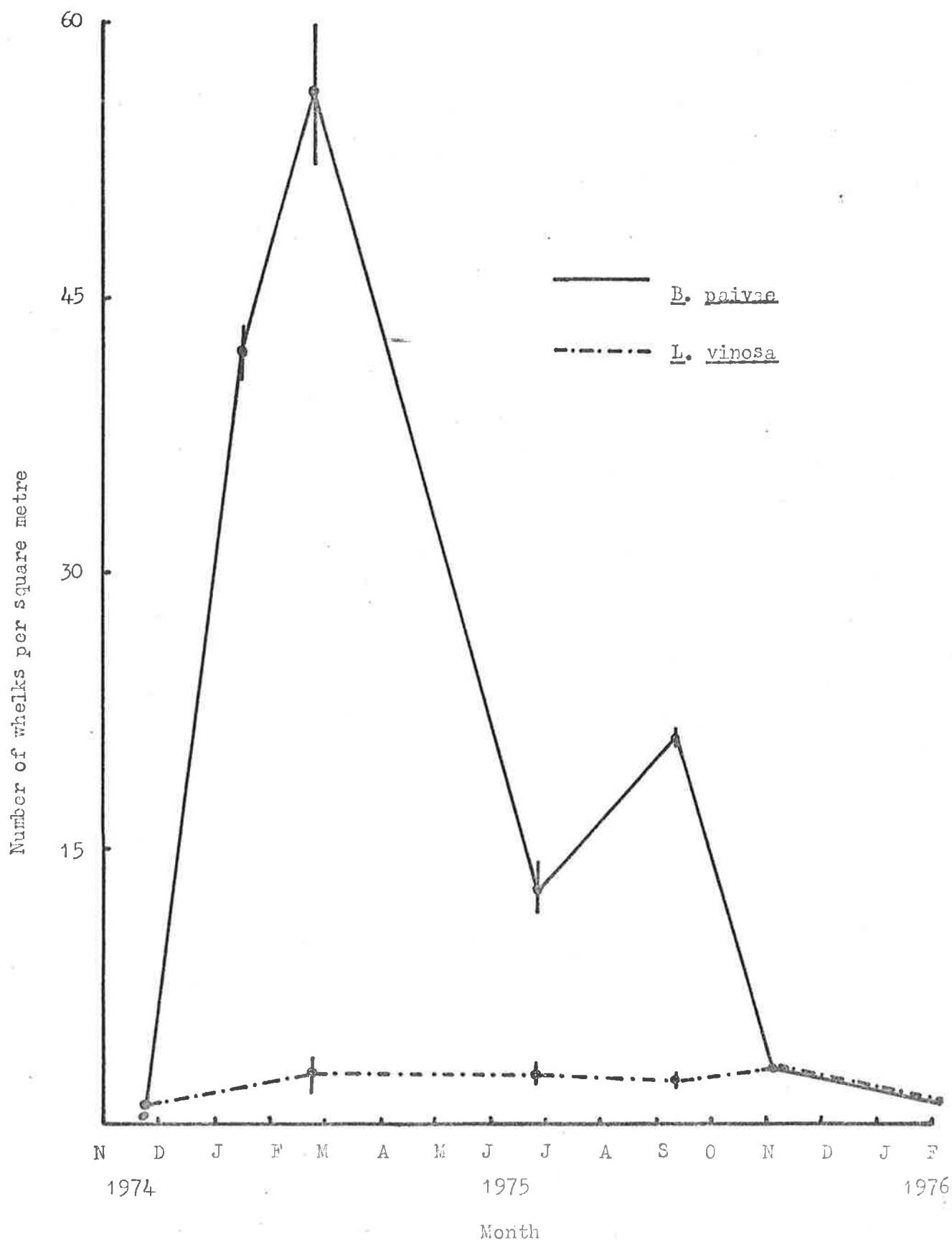


Figure 24. Number of *B. paivae* and *L. vinosa* per square metre in I patch between November 1974 and March 1976. Vertical lines indicate $\pm$ S.E.

5.2.4 Pneumatophore dynamics

The central area of the island was covered with small pneumatophores which were fairly densely packed. In figure 25 the mean length of the pneumatophores is shown. The short length enabled a square metre area to be surveyed without trampling the area as the pneumatophores do not obscure each other. Quadrats were taken on either side of a central line along the length of the island to minimize trampling. The large area allowed pneumatophores to be removed without greatly affecting the number in future survey quadrats. Estimates of pneumatophore density were made by taking five quadrats of one metre square and determining the average.

The density of pneumatophores between 22/11/74 and 9/2/76 is shown in figure 26. It was possible to determine the decline in the number of pneumatophores which were present before 24/2/75 as nearly all of these had barnacle shells on them and the new pneumatophores have no barnacles as no further settlement took place after this date. Pneumatophore death and replacement was most marked between June and November and only 36.7% of the old pneumatophores survived until February 1976. This mortality estimate is higher than for the inland patches. The island is however not as stable as the mangrove forest and is subject to strong currents and erosion.

5.2.5 B. amphitrite density and mortality

The density of B. amphitrite assessed in three different measures is shown in Table 17. The high density recorded on 22/11/74 is due to settlements in late August and September and no small barnacles less than 2mm in carino-rostral diameter are present. Slight settlement began in early December and an examination of the gonad states of large barnacles on 5/12/74 revealed a large proportion had fully developed larvae in the mantle cavities. Heavy settlement occurred before 14/1/75 and the density on pneumatophores peaked at 168.2 per metre of length. Settlement ceased by 24/2/75 and no further settlement was recorded throughout the next

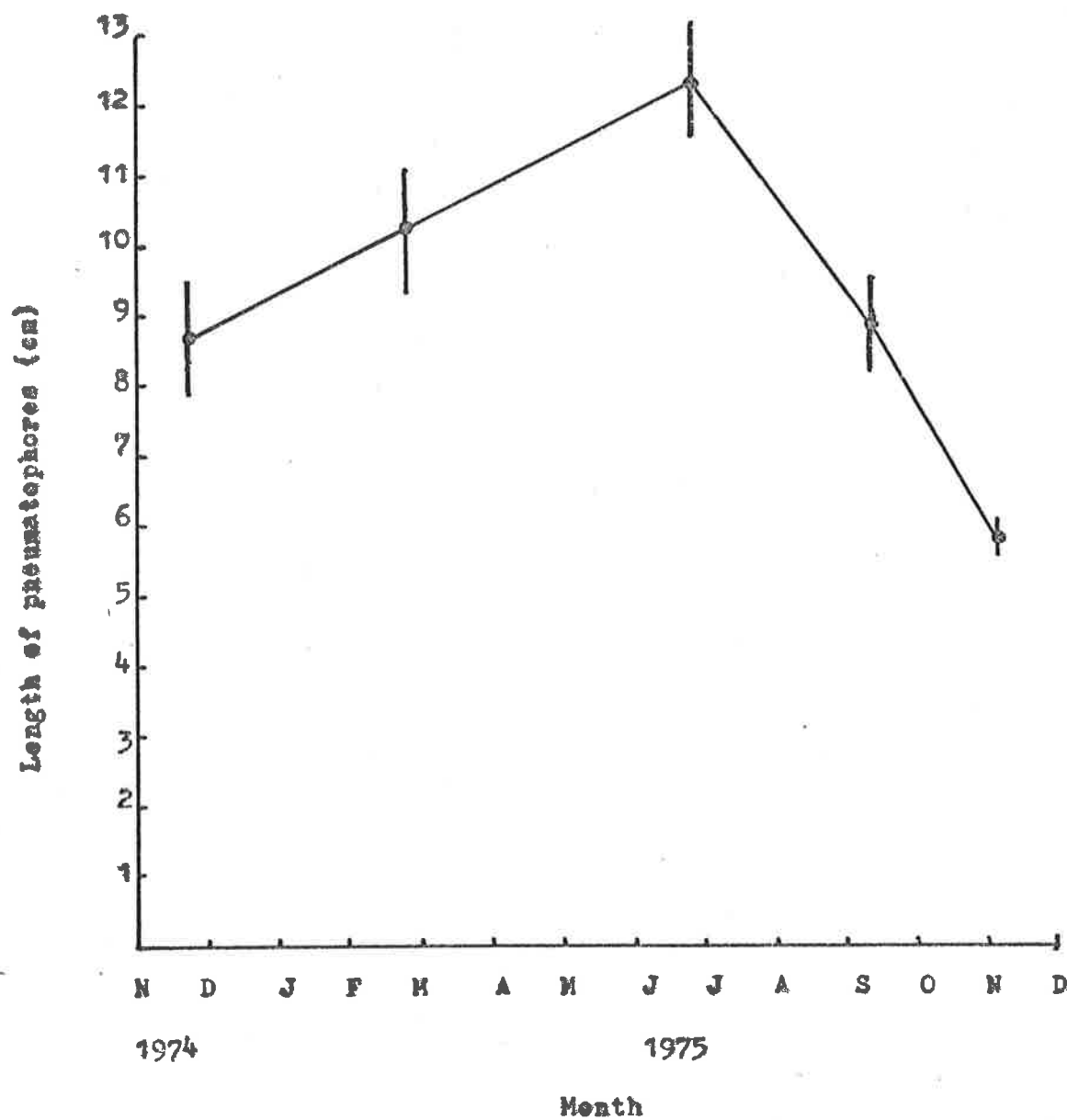


Figure 25. Length of pneumatophores ($\pm$ S.E.) in I patch.

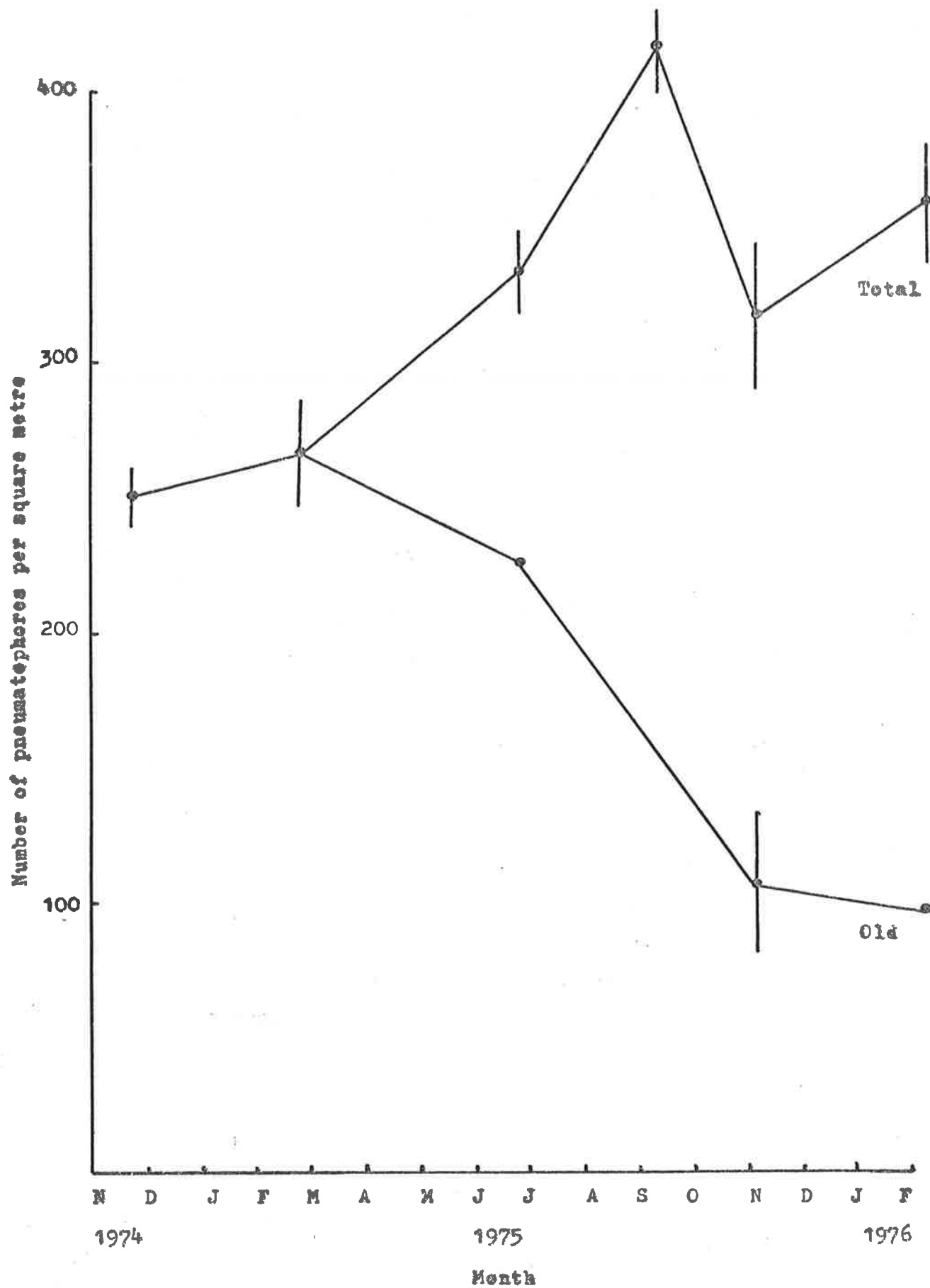


Figure 26. Number of pneumatophores per square metre ($\pm$ S.E.) in I patch between 22/11/74 and 9/2/76.

twelve months in this patch.

Extremely heavy mortality occurred in early June and the numbers recorded after June are so small as to be insignificant. The ratio of living to dead B. amphitrite shown in figure 27 is near zero after June reflecting the complete mortality which took place.

The number of B. amphitrite present on 24/2/75 would have been sufficient to support the maximum observed number of whelks for 46 weeks if predation was the only cause of mortality. Other causes of mortality such as pneumatophore death and intraspecific competition would however have eliminated many barnacles in this period.

Factors influencing the elimination of B. amphitrite between 24/2/75 and 25/6/75 are shown in Table 18. Mortality due to an unknown cause in early June probably would have eliminated the population irrespective of other causes of mortality.

TABLE 17. Density of B. amphitrite in I patch between 22/11/74 and 9/2/76.

Date	Number per square metre	Number per pneumatophore	Number per metre of pneumatophore
22/11/74	1,538	6.15	71.0
24/2/75	4,541	17.2	168.2
25/6/75	89	0.28	2.3
10/9/75	8	0.02	0.23
4/11/75	0	0	0
9/2/76	0	0	0

TABLE 18. Factors causing the near complete elimination of B. amphitrite, between 24/2/75 and 25/6/75 in I patch.

Number of B. amphitrite 24/2/75 = $4,541/m^2$

Number of B. amphitrite 25/6/75 = $89/m^2$

Survivors: = 1.96%

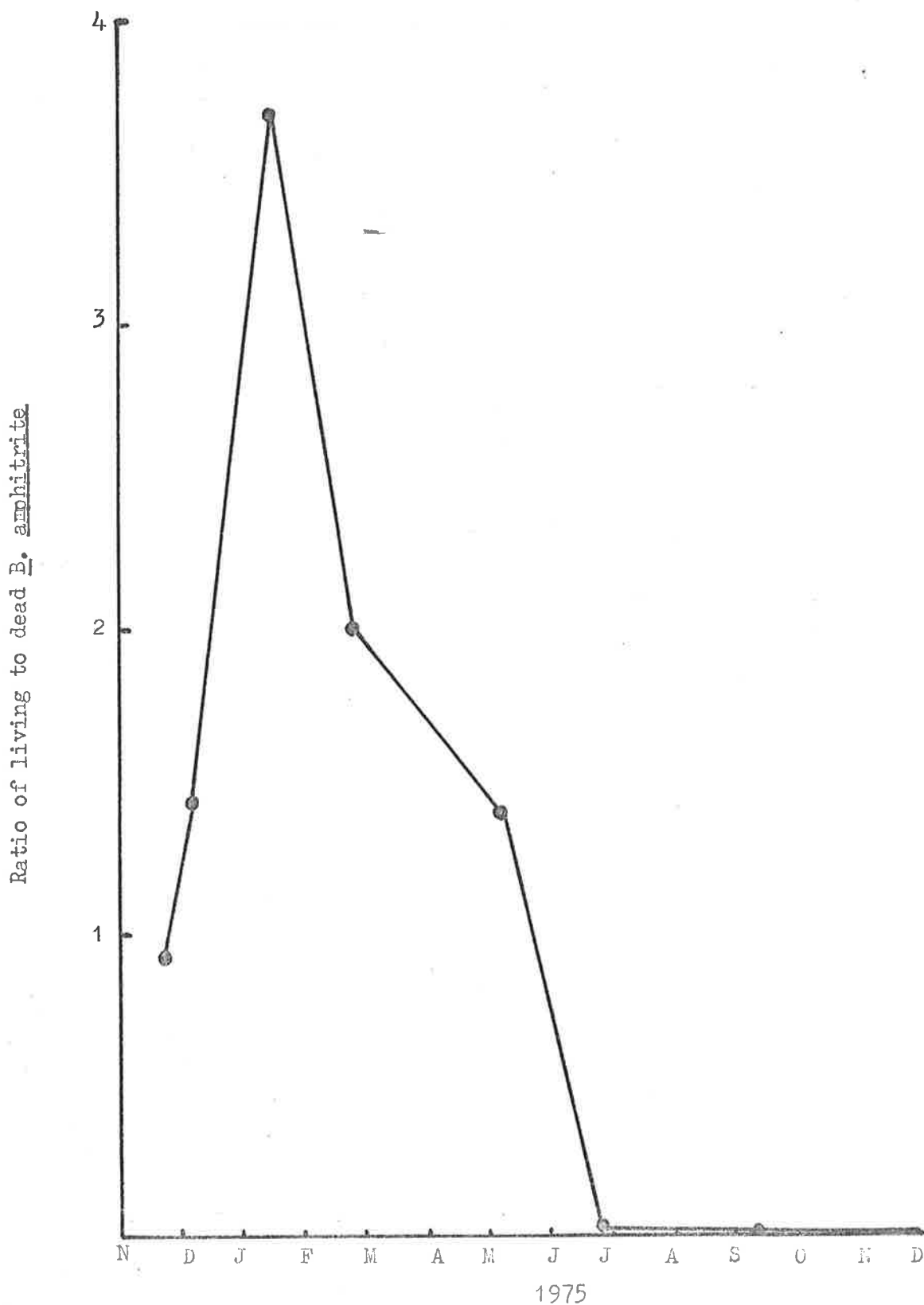


Figure 27. Ratio of living to dead B. amphitrite in I patch between November 1974 and December 1975.

Gastropod predators could eat $59 \times 17.29 \times 1.65 =$	$1,683/m^2$
Percentage consumed by gastropod predators =	37.06%
Percentage consumed by <u>L. vinosa</u> =	1.88%
Percentage consumed by <u>B. paivae</u> =	35.18%
Pneumatophore death =	14.8%
Mortality due to other causes =	46.18%
Number lost due to experimenter influence was negligible.	

5.2.6 E. modestus density and mortality

The density of E. modestus in I patch is given in Table 19.

Settlement was observed in November and December and there were a high proportion of the population 1mm or less in carino-rostral diameter during this period. The density decreased markedly in January due to interspecific competition with B. amphitrite. The heavy B. amphitrite settlement in January resulted in most pneumatophores being nearly covered with barnacles and as these grew they undercut and crushed the heavy concentration of E. modestus which had previously settled. Predation on B. amphitrite by whelks was not sufficiently heavy to prevent the competitive interaction. In early June massive mortality occurred and the population was virtually eliminated. No further restocking was observed before 9/2/76.

A summary of the factors causing mortality in the E. modestus population between 22/11/74 and 25/6/75 is shown in Table 20. Predation was an insignificant factor as no B. paivae were observed eating E. modestus and L. vinosa heavily preferred B. amphitrite and were not very abundant in any case. Sampling did not affect the results as the large area available for surveys allowed metre square quadrats to be left unsampled and not trampled for future surveys.

TABLE 19 Density of E. modestus in I patch between 22/11/74 and 9/2/76.

Date	Number per square metre	Number per pneumatophore	Number per metre of pneumatophore
22/11/74	6,100	24.4	281.8
24/2/75	2,706	10.3	99.9
25/6/75	70	0.21	1.71
10/9/75	8	0.02	0.34
4/11/75	0	0	0
9/2/76	0	0	0

TABLE 20 Factors causing the elimination of E. modestus between 22/11/74 and 25/6/75.

Number of <u>E. modestus</u> present	22/11/74	= 6,100 per square metre
Number of <u>E. modestus</u> present	24/2/75	= 2,706 per square metre
Number removed by competition		= 3,394 per square metre
		= 55.6%
Pneumatophore death	22/11/74 to 24/2/75	= 0
Predation by <u>B. paivae</u> and <u>L. vinosa</u>		= 0
Number of <u>E. modestus</u> present	25/6/75	= 70 per square metre
Number dying	24/2/75 to 25/6/75	= 2,636 per square metre
		= 97.4%
Pneumatophore death	24/2/75 to 25/6/75	= 14.8%

Conclusions

Death due to competition with <u>B. amphitrite</u>	= 55.6%
Death due to pneumatophore death	= 14.8%
Death due to unknown causes in June	= 29.6%

5.3 Discussion

Predation by L. vinosa is a significant cause of B. amphitrite mortality in the inland patches. L. vinosa has the potential to eliminate all B. amphitrite in the period between the last summer settlement and the subsequent spring breeding season. In the patches surveyed in this study this did not occur because L. vinosa responded to changes in the relative abundance of the two barnacle species. B. amphitrite, being the less abundant species, was subject to less predation than the more abundant E. modestus. Prey selection by L. vinosa in response to prey density is therefore an important factor for the survival of B. amphitrite between breeding seasons outside of refuge areas.

The inland patches were restocked by E. modestus at intervals of usually not more than two months. E. modestus, like B. amphitrite, suffered catastrophic mortality in the larval stages in spring 1975 and heavy mortality in the adults in June 1975. Nevertheless frequent settlement periods enabled a quick recovery in the abundance of this species in the patches. Predation by L. vinosa would not, by itself, have the potential to eliminate this species from the patches.

The density of L. vinosa in the patches remained fairly constant. The predator and its prey co-exist in the patches which are restocked by new settlements of barnacles. A gastropod predator, such as B. paivae, which aggregates in a prey patch can eliminate all prey before restocking.

Luckens (1970) has reported that Lepsiella scobina eats almost all barnacles in a patch before slowly moving to another area. Survival of the prey in this situation is dependent on spatial separation from the predator, continuous reproduction by the prey enabling resettlement of bare areas and preferential size selection by the predator.

The aggregation of B. paivae in I patch is almost certainly a response to the availability of a high concentration of prey. Aggregations of gastropod predators may be unrelated to feeding and could be due to such factors as breeding (Spight 1974) and protection from wave action

(Connell 1972).

High mortality in the adults of both species of barnacles was observed in June and the cause is unknown. The mortality was most marked in the lowest patch I and decreased with increasing height in the intertidal zone. Barnacles on branches and leaves of the mangrove trees were unaffected.

The mortality could be due to cold weather in early winter causing an unusually severe drop in water temperature. Pollutants from industry in the Port Adelaide area and pathogens are also possible causes. All of these would affect barnacles lowest in the intertidal zone more severely than those which are higher and hence inundated by water for shorter periods.

CHAPTER 6

Movement of *L. vinosa* in respect to barnacle patches

6.1 Introduction

In this chapter information on the mobility of *L. vinosa* and factors influencing the size of whelk populations in individual patches is presented. The effect of emigration and immigration on the *L. vinosa* population in individual patches was assessed. An attempt was made to determine the length of time *L. vinosa* remained in a patch, whether this varies between individuals and the extent to which the whelks move in the patches. The effect of seasons and prey abundance on *L. vinosa* mobility was also examined.

Food can be an important factor in determining the distribution of invertebrate predators (Connell 1972). Landenberger (1967) found that the local distribution of *Pisaster* was largely determined by food. The sea urchin *Strongylocentrotus franciscanus* exhibits higher rates of movement with increasing distances from kelp forests and they accumulate at the kelp forest border (Mattison et al 1977).

Few studies on movement have been reported for carnivorous gastropods. Phillips (1969) examined the movement of individual *Dicathais aegrota* over a six day period. Many of the animals remained stationary although some moved distances ranging from two to fifteen feet. Luckens (1970) has examined the movement of *Lepsiella scobina* in relation to prey patches.

The most extensive studies on the movements of intertidal molluscs have been made on limpet species. These studies have been concerned with homing (Breen 1971, Underwood 1977, Mackay and Underwood 1977), territorial behaviour (Stimson 1970 and Branch 1975) and population regulation (Frank 1965, Stimson and Black 1975, Black 1977).

6.2 Movement of marked individuals

6.2.1 Methods

L. vinosa in two pneumatophore patches were individually marked by painting numbers on them with nail polish. Care was taken not to disturb the whelks during painting and those which fell off the pneumatophore were discarded. Small plastic tags with corresponding numbers were pinned to the tops of the pneumatophores. The position of each L. vinosa on the pneumatophores was recorded.

Two groups of L. vinosa were examined in different patches. In the first experiment twelve L. vinosa were marked and the patch was re-surveyed after five days. In the second experiment twenty L. vinosa were marked and the patch was re-surveyed after five days and then again after a further seven days.

An attempt was made to find each marked whelk at each survey. If the whelk was found on another pneumatophore the distance it had travelled was measured. The new pneumatophore was then tagged so that the whelk's movement about the patch could be followed. The barnacles on the pneumatophores were counted and recorded according to species and whether alive or not.

At each survey the previous position of the whelk was examined. Attacks on barnacles can only be determined after the whelk has moved. If a barnacle is small it may also be obscured by a whelk so that identification cannot be made.

6.2.2 Results

The results obtained from the two experiments for movement over a five day period are combined in Table 20. The results obtained in the second experiment for a further seven days are shown in Table 21.

TABLE 20. Movement of L. vinosa over a period of five days. Total number of L. vinosa in experiment = 32.

a.	Number remaining on same pneumatophore =	8
	Previously recorded as eating =	5
	Previously recorded as not eating =	3

TABLE 20 (cont)

b.	Number changing pneumatophore but staying in patch =	7
	Previously recorded as eating =	1
	Previously recorded as not eating =	6
c.	Number leaving patch =	17
	Previously recorded as eating =	9
	Previously recorded as not eating =	8
	Average distance travelled in five days =	27.3cm
	(Only those which remained in patch).	

TABLE 21 Movement of L. vinosa over a period of twelve days.

Total number of <u>L. vinosa</u> in experiment =	20
Number leaving patch in first five days =	11
Number leaving patch in next seven days =	0
Number on same pneumatophore after twelve days =	1
Number changing pneumatophore but staying in patch =	8
Average distance travelled in twelve days =	70.3cm
(Only those which remained in patch).	

In a period of five days 53% of the L. vinosa left the patch in which they were marked and could not be found in the nearby mangroves. The remaining L. vinosa were still present after a further seven days. The proportion of L. vinosa remaining on the same pneumatophore was 53% of those staying in the patch after five days and 11% after twelve days. Distance travelled in the patch averaged 5.5cm/day over five days and 5.8cm/day over twelve days.

The animals which left the patch did consume barnacles before leaving. The proportion which had at least one feed was 52%. This group of feeders all left pneumatophores with living barnacles of the species which they were consuming. In some cases the other species was also present. Two of the non-feeding leavers however left pneumatophores on which all the barnacles were dead.

Many of the L. vinosa which remained in the patch also failed to eat all the available barnacles before moving to new pneumatophores. A high percentage, 63%, left pneumatophores with numerous prey and moved to pneumatophores with similar prey compositions. Nevertheless, four of the five eating L. vinosa which stayed on the same pneumatophore were attacking another barnacle. One of these L. vinosa was observed to be still on the same pneumatophore after a further six weeks. It was progressively eating each of the thirty E. modestus on the pneumatophore.

6.3 Movement of L. vinosa into and out of patches

6.3.1 Methods

The surveys reported in Chapter 7 were primarily designed to determine prey selection rather than immigration and emigration of individual L. vinosa. The results can however be used to obtain information on L. vinosa movement. There is a possibility that removal of all L. vinosa from the pneumatophores for marking resulted in artificially high emigration rates.

The continuous mark and recapture study over a twelve-month period in patches A, B and C provided information on the composition and density of the L. vinosa population. Changes in the colours used to denote feeding activities enabled the fate of whelks first captured during a particular survey to be followed and distinguished from other whelks.

Individual numbers were not used to distinguish between L. vinosa in these surveys as time was limited due to the tidal cycle. Removal of the whelks for twenty-four hours to mark individually may have introduced unacceptable experimenter influences.

6.3.2 Results

The percentage of L. vinosa observed at each survey which were present at previous surveys is shown in figure 28. Results for the three patches are combined.

No distinction is made between new arrivals at the previous survey

Percentage of L. vinosa from previous surveys present

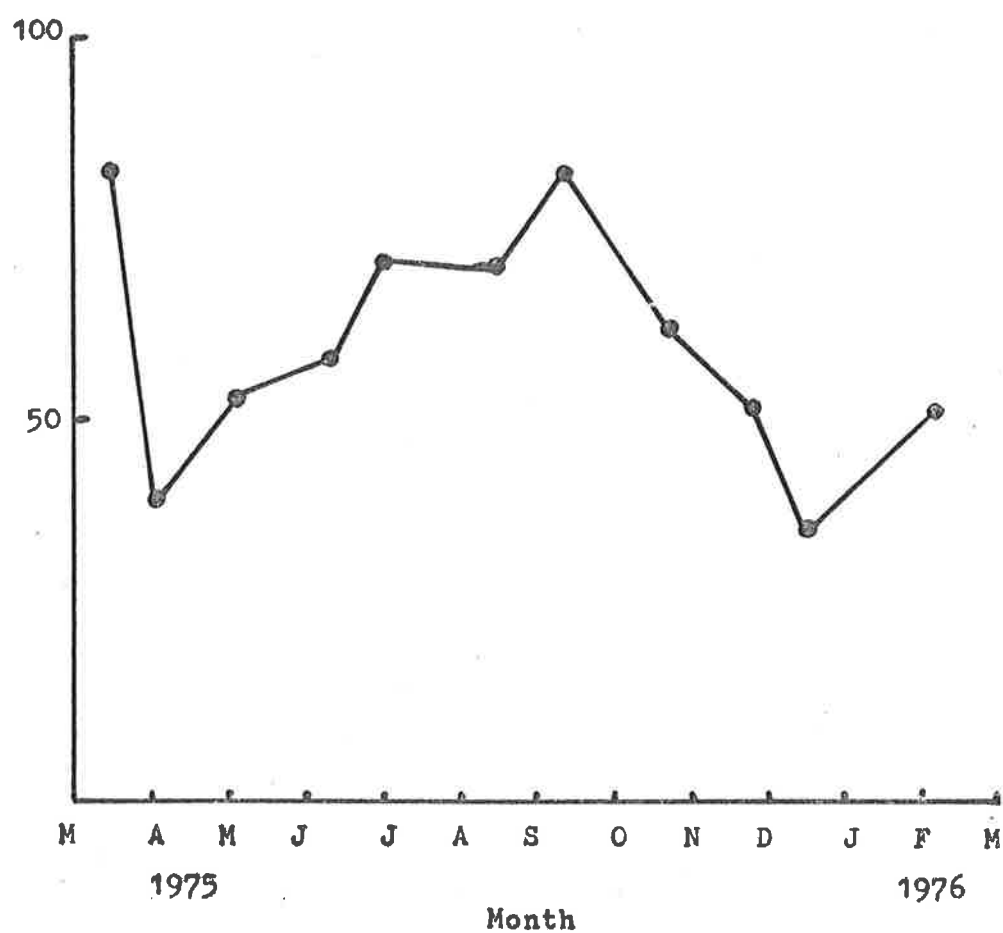


Figure 28. Recovery of previously marked L. vinosa.

and L. vinosa which had been observed in the patches for more than one survey.

There are two low points, one in early April and one in mid December. In the case of the April survey this is probably related to breeding as L. vinosa deposit their egg capsules below the low water mark. L. vinosa in the laboratory were observed laying egg capsules in March and April. A second breeding season in December may also explain the low recovery rate in this month. Egg capsules were not found in aquaria in December.

The combined number of L. vinosa in A, B and C patch outside of the breeding season, that is from May to December, is shown in figure 29. The number of "residents", that is those present at the previous survey, is also shown.

In the seven-month period there is very little change in the number of L. vinosa in the patches or in the number of "residents". The total inflow of L. vinosa balances the outflow between each of these surveys.

There is some evidence to suggest that the L. vinosa which constitute the "resident" group are only slowly replaced. In Table 22 the recapture rate of L. vinosa which had been in the patches for at least two months is calculated to be 94.9%. In contrast only 15.6% of L. vinosa first recorded in the previous survey one month earlier were recaptured.

L. vinosa classified as "residents" in late November 1975 only slowly left the patches. In early February 90.2% were still present and in mid-August 86.3% were recovered.

TABLE 22 Recovery of "residents" and new arrivals after a period of one month.

	<u>Present 2/5/75</u>	<u>Present 10/6/75</u>
<u>L. vinosa</u> in patches prior to 3/4/75 =	59	56
<u>L. vinosa</u> new in patches on 2/5/75 =	109	17

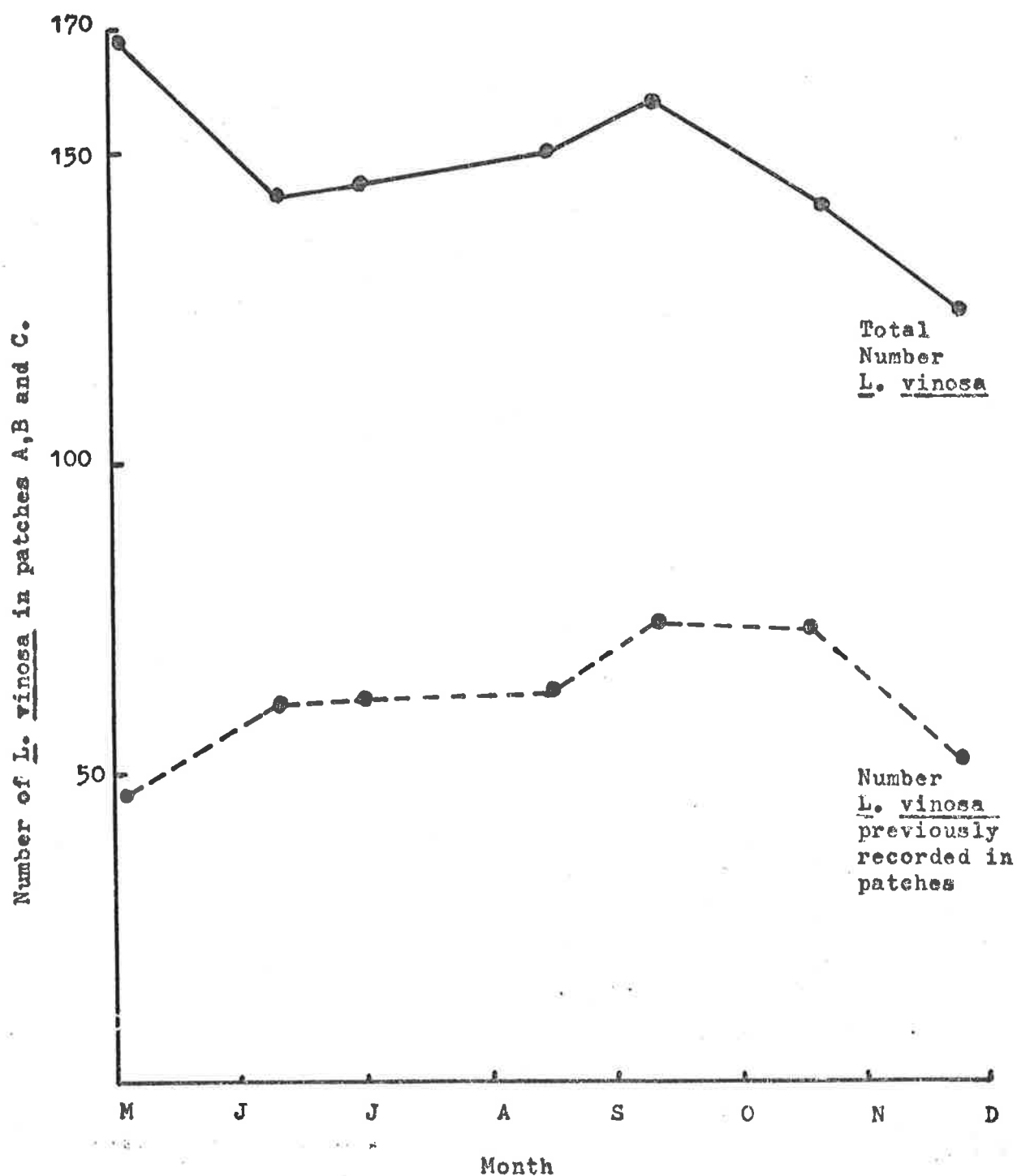


Figure 29. Number of L. vinosa in patches A, B and C between May and December 1975.

6.4 Discussion

Two conclusions can be drawn from the results. Firstly the predator density in the patches remains fairly constant, despite considerable immigration and emigration. This indicates that movement maintains local density in a prey patch. Secondly the whelks show marked individual differences in mobility and can be divided into two behavioural types. Highly mobile whelks which remain for only a few meals in a patch can be considered as "wanderers". Those whelks which remain in a patch for long periods can be considered as "residents".

Residents do slowly leave the patch and a small percentage of wanderers become residents. The whelks which were examined were mainly adults and the comparative rarity of juveniles prevented useful information on their mobility being obtained. Fluctuations in prey density affected neither the total predator density nor the number of residents.

There are numerous reports in the literature, particularly in respect to vertebrates, of animal populations consisting of residents and wanderers (Andrewartha and Birch 1954, Wilson 1975, Errington 1946, Howard 1960, Clough 1965). The "wanderers" are often considered to be those which are in some sense in excess (Errington 1946), the "losers" in territorial contests for the optimum living space (Wilson 1975).

Individual differences in respect to movement have been reported in limpets with regard to homing and territorial behaviour. Breen (1971) found that in Acmaea digitalis there are two behavioural types with respect to homing. Over a period of six months some animals continuously returned to a home site while others wandered over the study area. Similar results have been obtained for Cellana tramoserica (Underwood 1977) and Patella granularis (Branch 1975).

Mackay and Underwood (1977) found that limpets can stop homing and that moving limpets could become homers. Branch (1975) states that it is the smaller Patella granularis which are predominantly the wanderers.

limpets (Breen 1971, Mackay and Underwood 1977).

Lomnicki (1969) found individual differences in the mobility of members of a land snail population, Helix pomotia, during a mark and recapture study. In eight surveys those snails found in the previous surveys had a much higher probability of being found again. The snails are not aggressive or territorial and the more mobile members would appear to be more subject to mortality from predation, drought, frost and accidental death as they stay on the surface more often.

The local density of limpets may be regulated by dispersion. Frank (1965) found that Acmaea digitalis adjust their population densities by movements. Stimson and Black (1975) altered the numbers of limpets on pier pilings and found that the density on experimental pilings returned to that of the control pilings. They suggested that density dependent vertical migrations, cannibalism of the newly settled young and larval selection of substrate might be important factors. Stimson (1970) reports that individual Lottia gigantea live in one area for prolonged periods and defend the area against encroachment by members of their own species. Defence of algal territories has also been reported in Patella longicosta (Branch 1971).

Black (1977) however reports that in Patelloidea alticostata migration did not act in a density dependent manner. The convergence of the number of limpets towards constant density over a period of two years could be attributed to mortality.

Generalisations about the feeding behaviour of L. vinosa once on a particular pneumatophore are difficult to make on the basis of the data. There is however an indication that a high proportion of whelks eat only one or a few barnacles. This occurs despite other prey being present. A high rejection rate following thorough prey evaluation was observed in aquaria (section 4.2). It may be more efficient for a predator which spends so long drilling one food item to be highly selective before

beginning its attack. The wheelks, in many cases, appear to change pneumatophore frequently as if to increase the number of prey evaluated before initiating an attack.

CHAPTER 7

Prey selection by *L. vinosa* under natural conditions in the field.

7.1 Introduction

The whelk *L. vinosa* is naturally found in its greatest abundance in clearly defined pneumatophore patches which have high prey concentrations compared to the surrounding area. In this chapter results obtained from surveys over a period of a year in eight of these patches will be presented. Determination of prey selectivity of invertebrate marine predators by the simple technique of finding a large number of them and scoring the prey which they are in the process of attacking is common in the literature (Connell 1961, Feder 1959, Paine 1963 and 1966, Phillips 1969 and Menge 1973). In this section the prey selection of the predator population will be related to accurate measures of the prey species abundance.

My aims are to determine whether the predator population responds to changes in the abundance of its prey and if so what is its response. Furthermore the aspects of prey abundance which influence the response are investigated to determine if relative or absolute density of the prey species is important or if these factors interact. Finally the mechanisms by which the predator population changes its prey selection as prey abundance changes are investigated.

7.2 Methods

L. vinosa are immobile at low tide and are normally found either sitting on a pneumatophore or on barnacles which have settled on the pneumatophores. The feeding preference of *L. vinosa* in each patch was determined by finding all *L. vinosa* in the patch and scoring them as consuming *B. amphitrite*, *E. modestus* or not eating.

The predators were only classified as attacking a prey if there were signs of drilling or if the barnacle was being consumed. In those cases where the whelk was sitting on the barnacle but no evidence of drilling was apparent the whelk was scored as not eating. Observations in the laboratory indicated that many whelks spend considerable time evaluating a

barnacle only to leave it for another without initiating an attack. It was therefore felt that a whelk merely sitting on a barnacle at low tide is not sufficient evidence to classify it as an attack. Whelks may of course leave a barnacle after drilling without consuming it, but, this was infrequently observed in the laboratory and in any case the damage done to the barnacle would cause its subsequent death.

It was necessary to remove the whelk from the barnacle to determine if an attack was taking place and also to determine the species of barnacle particularly if the barnacle was small and hence partially concealed. Care was required to avoid damage to the proboscis which was sometimes found extended into the barnacle's mantle cavity. In general gentle tapping or rocking of the whelk caused the proboscis to be withdrawn and hence not be damaged. The two species of barnacles are easily distinguished in the field.

All L. vinosa which were found in a patch were classified and marked according to feeding preference. Nail polish was found to adhere for sufficiently long periods and different colours were used to denote prey selection and feeding activity. The positioning of the nail polish marks on the shell could be used to denote successive surveys. It was thus possible to determine changes in prey selection by individual whelks between different surveys. Individual numbers were not used.

After classifying and marking, the whelks were spread randomly throughout the patch from which they were collected. Whelks could not be reattached to the pneumatophores and no attempt was made to position individual whelks near the pneumatophores from which they were collected. Immersion during the following tidal cycle invariably saw the whelks climb onto pneumatophores and recommence the search for prey. No apparent increase in the loss of predators from a patch due to removal during surveys was observed.

The relative and absolute density of the barnacle species were

determined for each patch as described in section 5.1.2. The number of barnacles per unit length of pneumatophore is used for density measurements as it is the most accurate measure and also the factor most likely to be monitored by the whelk.

7.3 Predators response to changes in relative prey density

The prey selection of L. vinosa in eight patches was followed during 1975 to determine the reaction of the predators to changes in the relative abundance of the two prey species. The relationship between the relative availability of B. amphitrite, the preferred prey species, in the patches and the proportion it constituted in the diet of L. vinosa is shown in figures 30 to 37. The chi-square test is used to determine if L. vinosa is feeding proportionally with regard to the relative abundance of the two prey species in each individual patch. Correlation analysis would not provide appropriate information on whether the whelks switch, feed proportionally or satisfy other possible hypotheses.

The results obtained for A and B patch are analysed in Table 23. The number of whelks observed eating B. amphitrite on thirteen occasions throughout the year is compared with the expected number of whelks which should be eating this species if they fed proportionally, with $C=1.26$. Evidence that the "C" value is 1.26 is given in section 9.3.3.

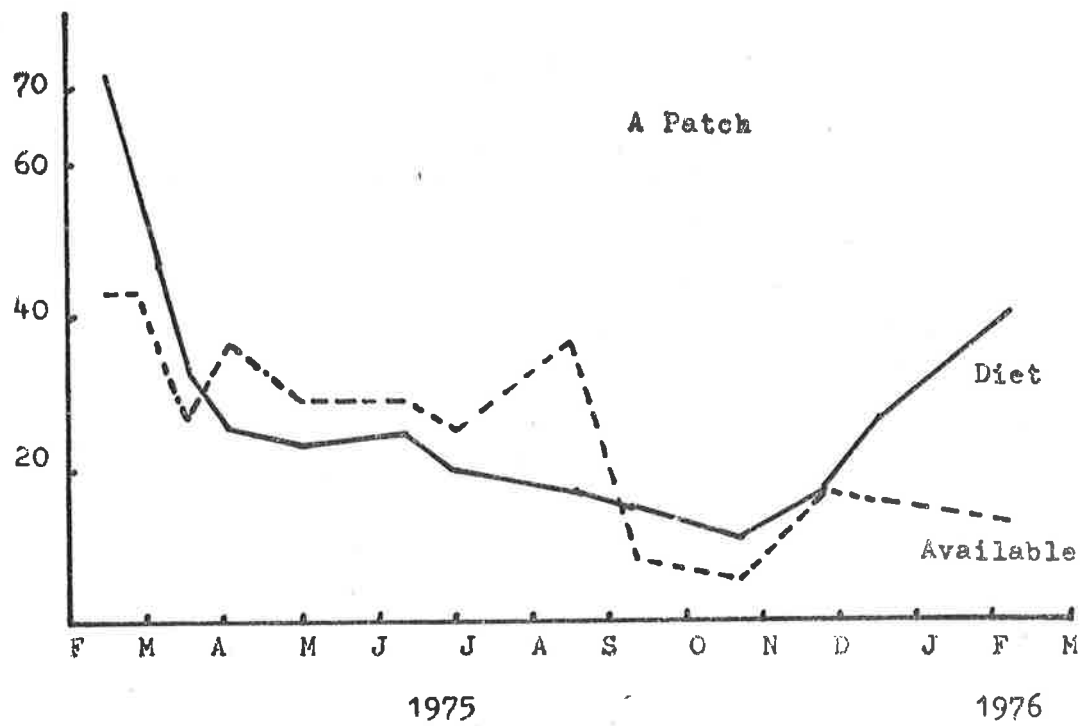
In the case of B patch the association between expected and observed prey selection is less than the critical value for χ^2 . The proportion of B. amphitrite varied from 3.1% to 15% of the available barnacles. For A patch the critical χ^2 value is not exceeded. The proportion of B. amphitrite varied from 43.8% to 5.5% of the available barnacles and there is no statistical evidence to suggest that the whelks did not feed proportionally with $C = 1.26$.

Figure 30. Percentage of B. amphitrite in the barnacles in A patch and the percentage of B. amphitrite in the diet of L. vinosa feeding in this patch.

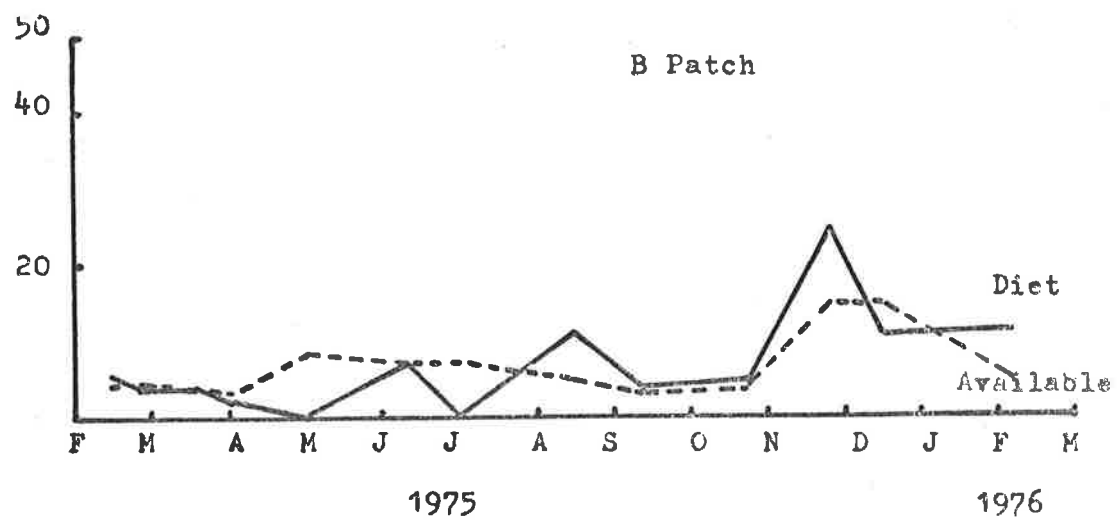
Figure 31. Percentage of B. amphitrite in the barnacles in B patch and the percentage of B. amphitrite in the diet of L. vinosa feeding in this patch.

Figure 32. Percentage of B. amphitrite in the barnacles in C patch and the percentage of B. amphitrite in the diet of L. vinosa feeding in this patch.

Percentage of B. amphitrite



Percentage of B. amphitrite



Percentage of B. amphitrite

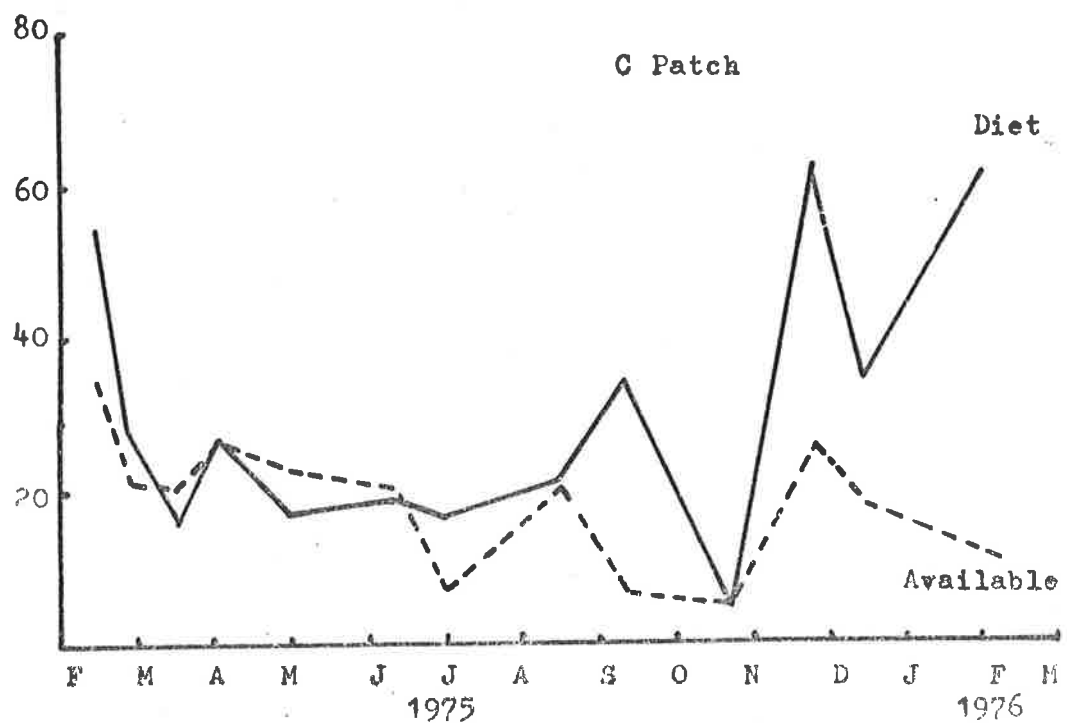
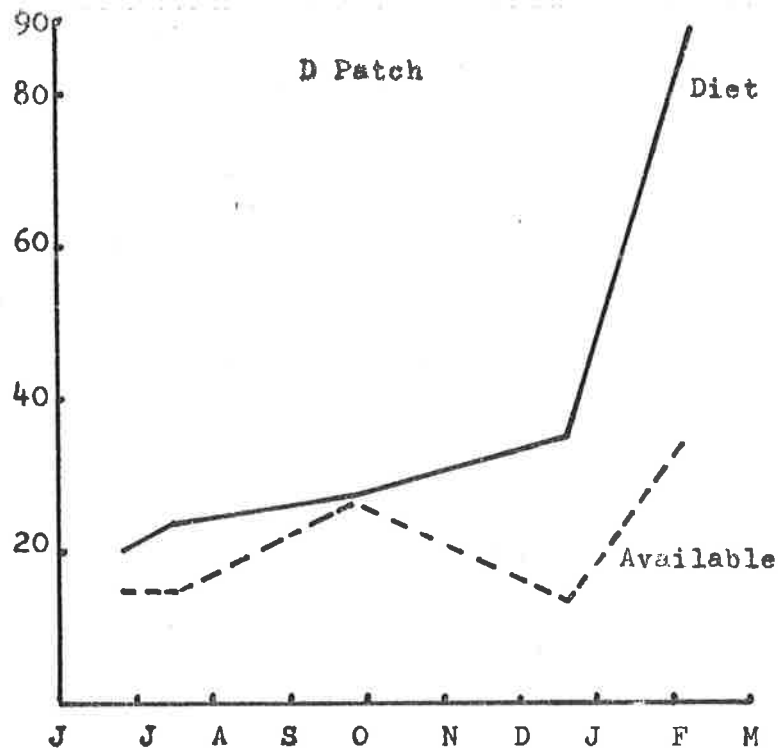


Figure 33. Percentage of B. amphitrite in the barnacles in D patch and the percentage of B. amphitrite in the diet of L. vinosa feeding in this patch.

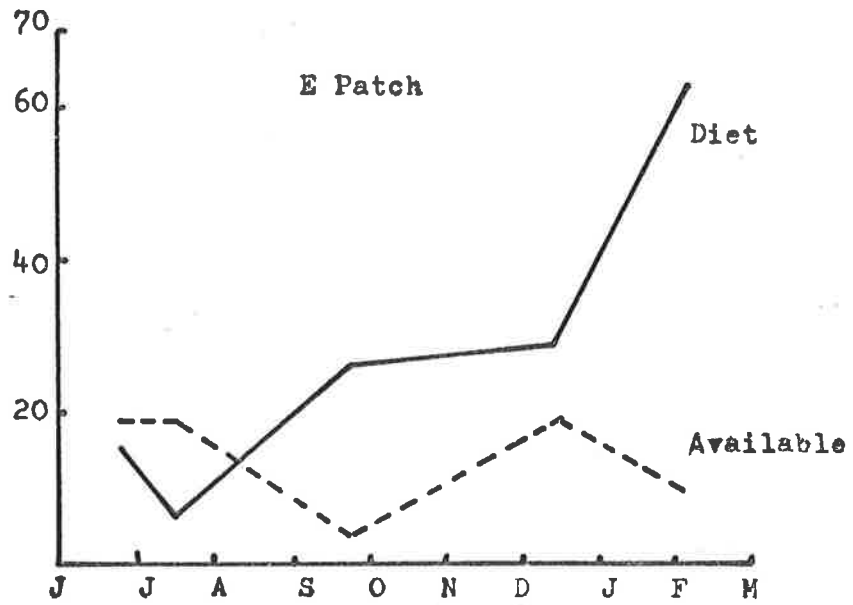
Figure 34. Percentage of B. amphitrite in the barnacles in E patch and the percentage of B. amphitrite in the diet of L. vinosa feeding in this patch.

Figure 35. Percentage of B. amphitrite in the barnacles in F patch and the percentage of B. amphitrite in the diet of L. vinosa feeding in this patch.

Percentage of B. amphitrite



Percentage of B. amphitrite



Percentage of B. amphitrite

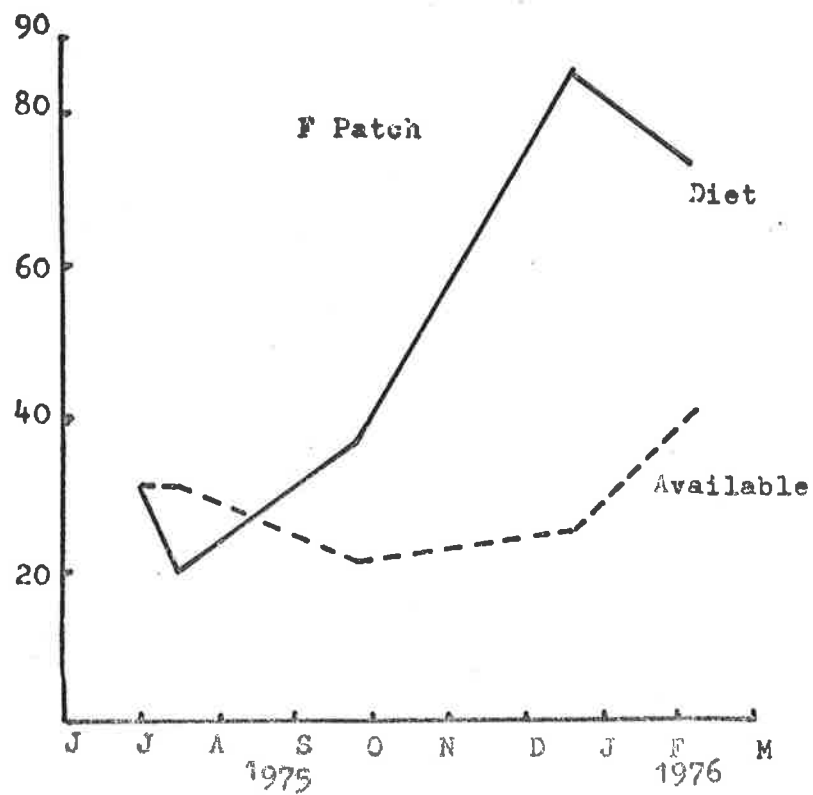


TABLE 23. Comparison of the observed and expected number of whelks feeding on B. amphitrite in A and B patch.

Patch	Number of observations	D.F.	Critical χ^2 (P=0.05)	χ^2 for C=1.26
A	13	12	21	20.73 n.s.
B	13	12	21	6.46 n.s.

The results obtained for patches C to F are shown in Table 24. In these patches spring settlements of B. amphitrite occurred. A peak in November for B. amphitrite density in C patch is shown in figure 16.

Prior to this settlement the relationship between available B. amphitrite and the proportion it constituted in the diet of L. vinosa appears close and is not significantly different to the expected on the basis of χ^2 tests listed in Table 24.

TABLE 24. Comparison of the observed and expected number of whelks feeding on B. amphitrite in C,D,E and F patch prior to September.

Patch	Observations	D.F.	Critical (P=0.05)	χ^2 for C=1.26
C	8	7	14.1	4.24 n.s.
D	3	2	5.99	0.39 n.s.
E	2	1	3.84	1.63 n.s.
F	3	2	5.99	2.0 n.s.

The final survey, made in February 1976, shows an unusual discrepancy between prey selected and prey available in all patches except B compared to the previous twelve months of close association. The absolute density of B. amphitrite was not unusually high. I would expect that as in the case of A and C patch in the previous summer that the whelks were slow

to change back to feeding on E. modestus following a summer B. amphitrite settlement. That is once they changed to feeding on B. amphitrite a subsequent E. modestus settlement, which again lowered the relative abundance of B. amphitrite, was not responded to immediately.

In field cage experiments, reported in section 9.3, a difference in the time required for L. vinosa to respond to a major change in relative density was found to depend on which species the whelk had been feeding on. It will be shown that a whelk feeding on E. modestus changes quickly to B. amphitrite if it becomes far more abundant but the reverse change takes many weeks. I do not think that the higher B. amphitrite selection in February is some unknown "summer" effect as some of these field cage experiments were conducted in winter.

In G patch the observed number of whelks feeding on B. amphitrite is greater than expected on the basis of the relative abundance of B. amphitrite with $C = 1.26$ ($\chi^2 = 134.1$, $df=5$, $P<0.01$). Heavier than expected predation on B. amphitrite is also found in I patch ($\chi^2 = 279.3$, $df=6$, $P<0.01$). This result is not consistent with switching, however, as the available percentage of B. amphitrite in the patches is below 39.6 in a number of readings.

7.4 Influence of absolute density of preferred prey species on the percentage of L. vinosa eating that species.

L. vinosa may be primarily influenced in the selection rate of B. amphitrite by the absolute abundance of this species rather than the relative abundance compared to E. modestus. The predator could simply concentrate its attacks on the preferred prey and only reduce its attack rate as the density, and hence frequency of encounter, decreased. This hypothesis is examined in the case of high and moderate densities.

7.4.1. High densities.

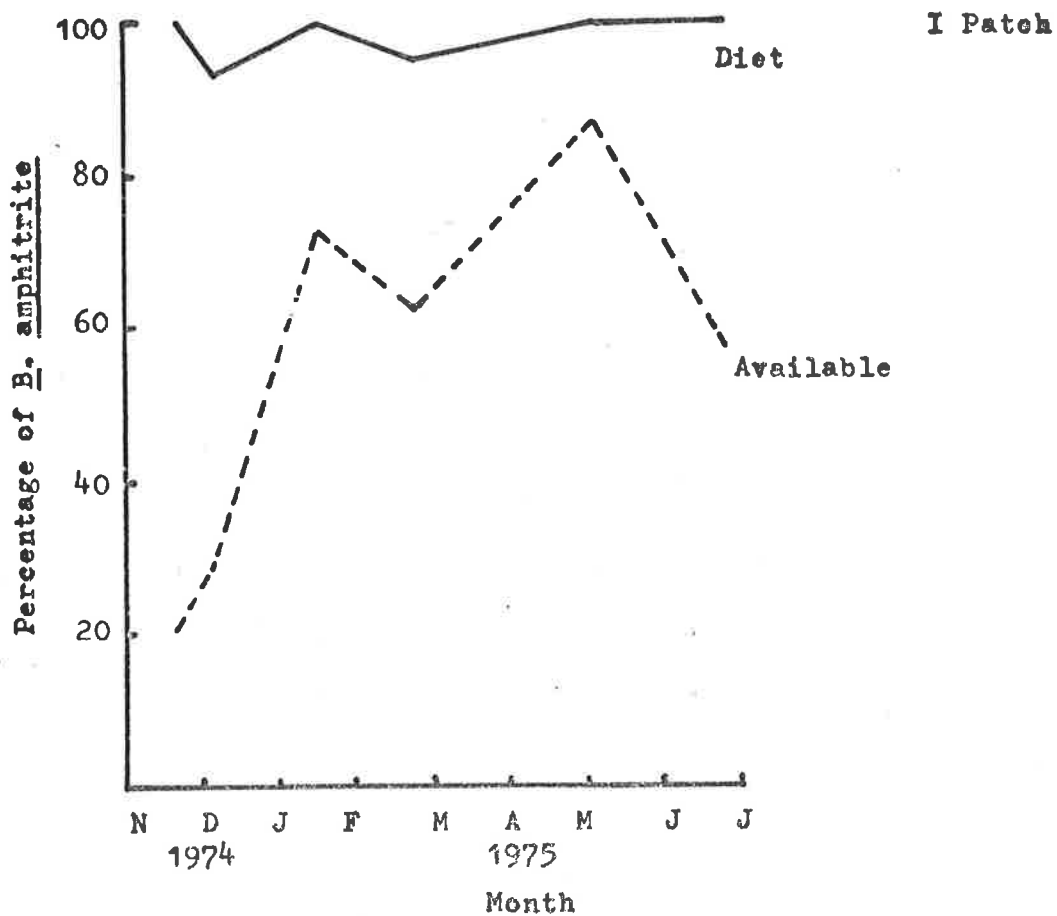
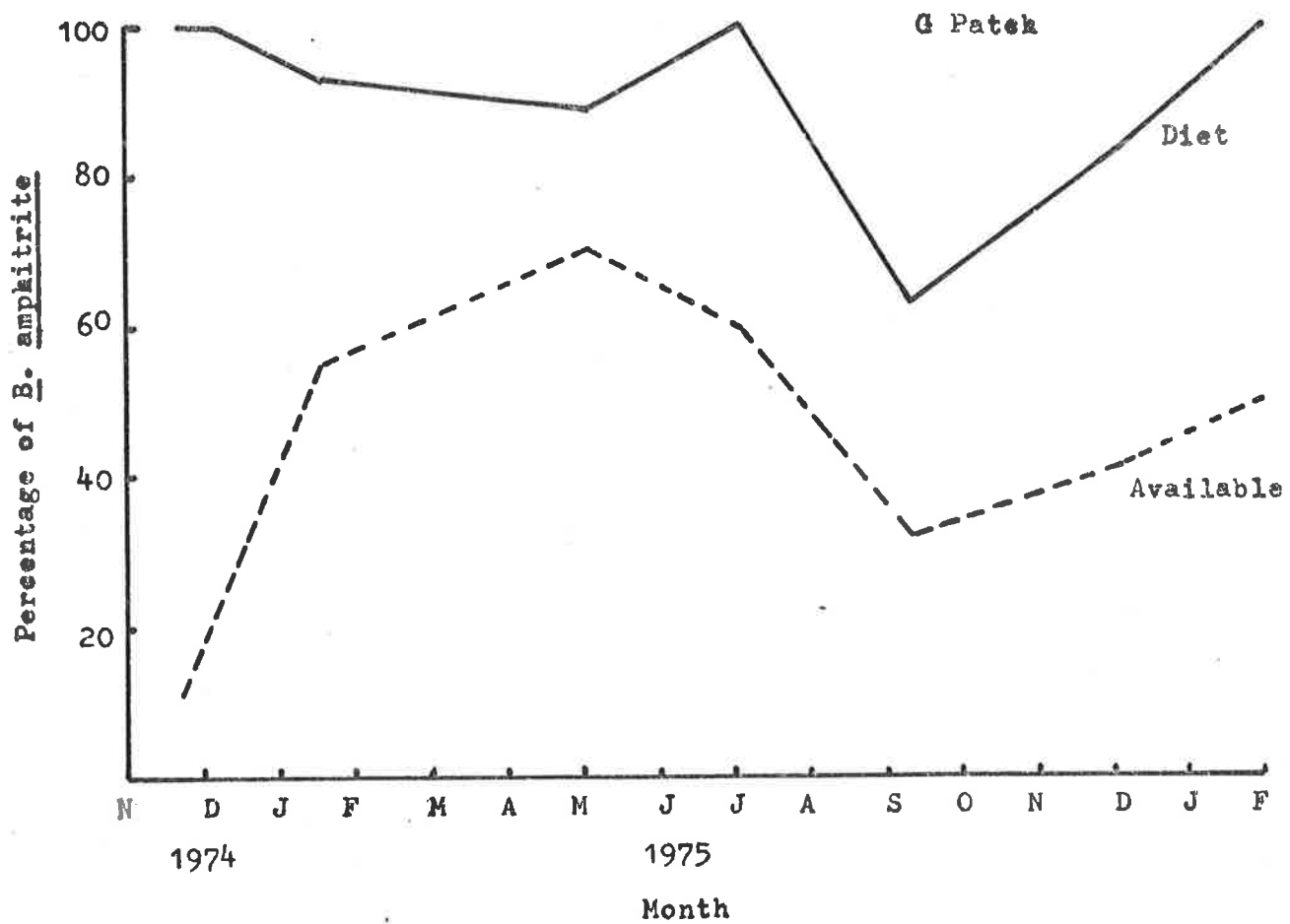
At high B. amphitrite densities, that is above 25 per metre length of pneumatophore, L. vinosa appears to concentrate its attacks on B.

amphitrite irrespective of relative abundance. This situation was observed in two patches, G and I, which were on a small island and at the seaward fringe of the mangroves. Observations of the seaward fringe barnacle zone in G are I believe, typical of this zone. In I patch the attack rate on B. amphitrite was never less than 93% despite an availability range of 20% to 87% shown in figure 37. Figure 36 shows a similar high percentage of B. amphitrite being attacked in G patch, except for one reading in September, and a fairly complete disregard for variation in relative abundance.

The majority of observations made in these patches corresponded to periods where the relative abundance of B. amphitrite was greater than 39.6% which is the expected mid-point of the sigmoid curve if switching occurs for a predator with a C value of 1.26. That is for two-thirds of the observations heavier than expected predation on B. amphitrite would occur if the predator switches due to relative abundance. Nevertheless the preference for B. amphitrite is always very high and was 100% on readings of relative availability as low as 11 to 20%.

Figure 36. Percentage of B. amphitrite in the barnacles in G patch and the percentage of B. amphitrite in the diet of L. vinosa feeding in this patch.

Figure 37. Percentage of B. amphitrite in the barnacles in I patch and the percentage of B. amphitrite in the diet of L. vinosa feeding in this patch.



7.4.2. Moderate Densities

The density of B. amphitrite seldom exceeded 25/metre length of pneumatophore in the inland patches A to F. In these patches L. vinosa ate B. amphitrite in proportion to B. amphitrite's relative abundance compared to E. modestus if the C value is 1.26. Nevertheless it is possible that changes in the absolute density of B. amphitrite could be the factor which generates this relationship. Factors such as settlement and mortality of this species directly affect both absolute and relative abundance and could cause both to rise and fall at the same time.

A total of 46 surveys were carried out in patches A to F when the abundance of B. amphitrite was below 10/metre length of pneumatophore. The percentage of B. amphitrite in the diet of L. vinosa is plotted against the number of B. amphitrite per metre of pneumatophore in figure 38, and against the percentage of B. amphitrite which are available in figure 39.

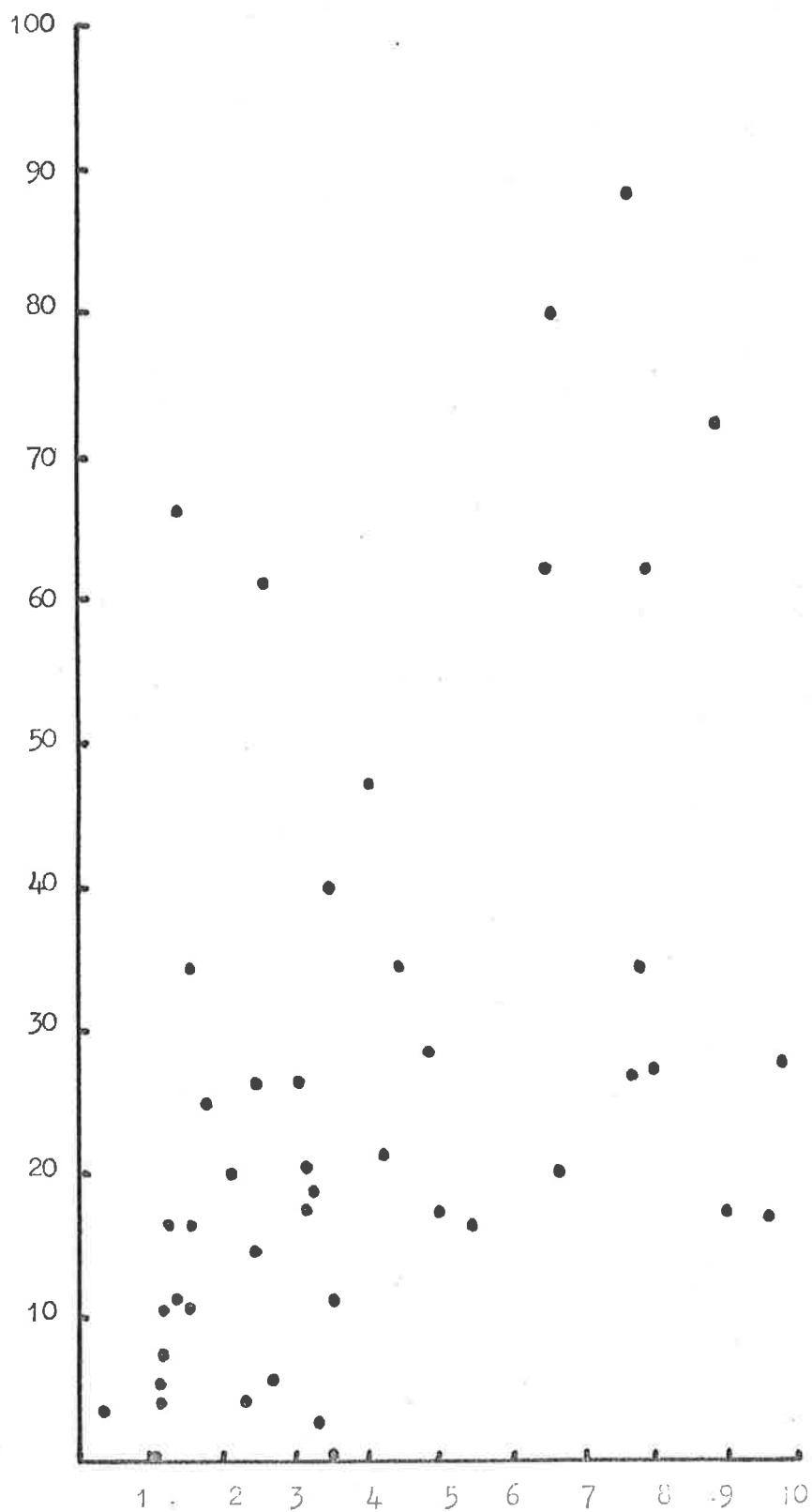
The results, in both cases, cannot be analysed using Model I regression as the dependent as well as the independent variable are subject to error (Sokal and Rohlf 1969). Model II regression is appropriate but the data requires the arcsine transformation. Unfortunately the results obtained when transformed data are used are not intuitively easy to interpret.

The results were therefore analysed using the Spearman rank correlation coefficient. There is a significant association between the percentage of B. amphitrite in the diet and both the number of B. amphitrite per metre of pneumatophore ($r_s=0.53$, $t=4.1$, $n=46$, $P<0.01$) and the percentage of B. amphitrite which are available ($r_s=0.66$, $t=5.85$, $n=46$, $P<0.01$).

The results therefore fail to indicate which factor is important at moderate densities. Field cage experiments in which the densities are controlled by the experimenter are required and will be reported in chapter 9.

Figure 38. Percentage of L. vinosa feeding on B. amphitrite
at different densities of B. amphitrite.

Percentage of L. vinosa eating B. amphitrite



B. amphitrite per metre of pneumatophore

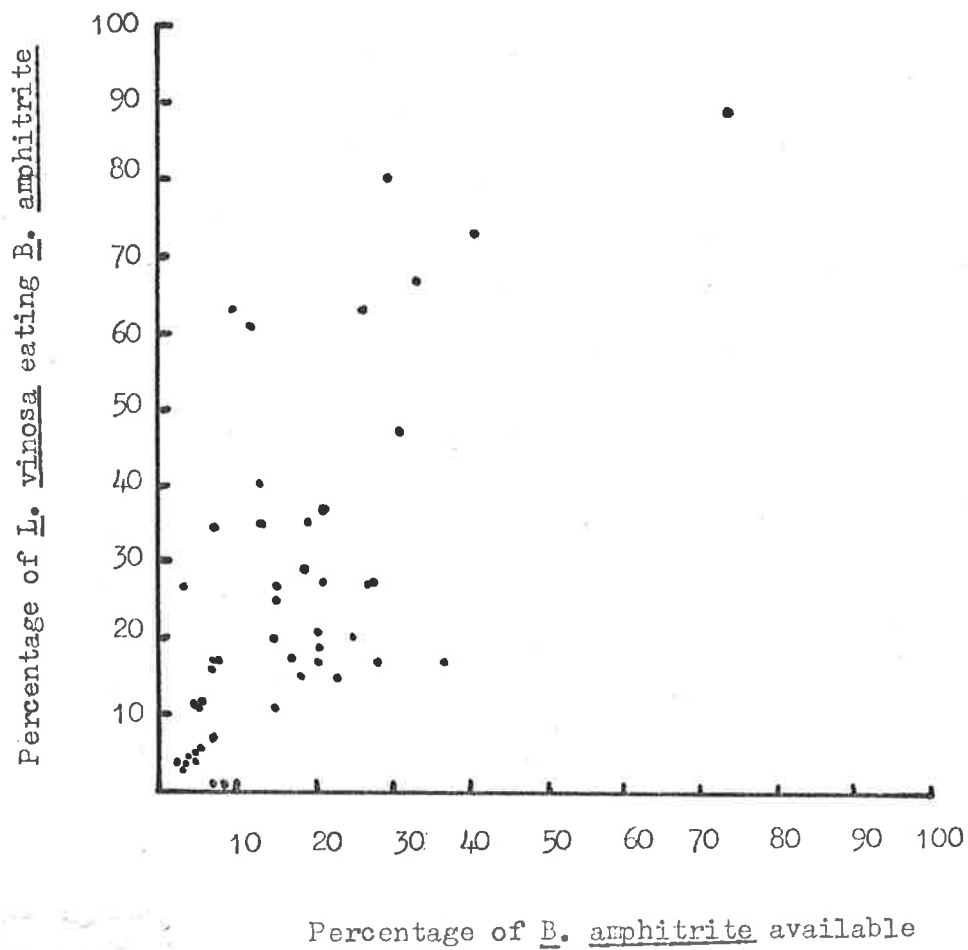


Figure 39. Percentage of L. vinosa feeding on B. amphitrite at different relative densities of B. amphitrite in the barnacles available.

7.5 Examination of possible mechanisms by which the L. vinosa population could adjust to changes in the relative abundance of barnacle species.

In patches A, B and C the whelks fed on the two species in proportion to the relative abundance of each species. The feeding preferences of the whelks must change in response to changes in the prey species densities to produce this result. There are a number of possible mechanisms or combinations of mechanisms by which the whelk population of a patch could modify its feeding preference and these are now considered in turn.

The results reported in this section come only from patches A, B and C which were surveyed thirteen times between February 1975 and February 1976 at roughly four week intervals. Patches D, E and F were surveyed less frequently and the results will not be used.

7.5.1. Change in prey species selected by individual L. vinosa.

E. modestus was more abundant than B. amphitrite in all surveys in patches A, B and C and the effect of this on the likelihood of individual L. vinosa changing prey species in consecutive surveys can be examined by 2x2 contingency tables. L. vinosa marked as feeding on B. amphitrite or E. modestus in one survey can be classified according to which species they were feeding on in the following survey. This was done for twelve consecutive surveys in each patch and the results are shown in Table 25.

TABLE 25. Comparison of likelihood of L. vinosa consuming B. amphitrite or E. modestus after being observed feeding on either E. modestus or B. amphitrite during the previous survey.

Patch	First Survey	Second Eating <u>B. amphitrite</u>	survey Eating <u>E. modestus</u>	χ^2 P 0.01
A	<u>E. modestus</u> eater	13	70	6.34 significant
	<u>B. amphitrite</u> eater	13	20	
B	<u>E. modestus</u> eater	9	137	5.85 significant
	<u>B. amphitrite</u> eater	4	10	
C	<u>E. modestus</u> eater	12	42	0.003 n.s.
	<u>B. amphitrite</u> eater	5	15	

The χ^2 values indicate that there is a significant difference in the prey species chosen in the second survey depending on the species chosen in the first survey in patches A and B. E. modestus eaters, in these patches, are more likely to choose E. modestus in the following survey than are B. amphitrite eaters. This result is consistent with switching and could be due to "ingestive conditioning" to the more abundant prey species.

In patch C, ^{the} χ^2 value is not significant. This result is consistent with a hypothesis of non-selective or random feeding as the species chosen is independent of the previous species chosen.

A direct statistical analysis for switching is not possible as the number of E. modestus eaters recorded during most surveys is too low for a meaningful comparison with the expected proportion of L. vinosa feeding on E. modestus given $C = 1.26$.

7.5.2. Emigration as a possible factor influencing predation on the two prey species.

The overall prey selection by the L. vinosa population would change if L. vinosa which fed on each prey species emigrated at different rates. In the period of this study there was a continuous decline in the relative abundance of B. amphitrite. If L. vinosa which fed on B. amphitrite showed a higher rate of emigration from the patches than E. modestus eaters then the prey selection of the L. vinosa population would reflect the decline in B. amphitrite abundance.

To examine this possibility L. vinosa which were feeding on each prey species at one survey were classified as having either left or stayed in the patch at the following survey. The results are shown in Table 26.

TABLE 26. Comparison of the likelihood of L. vinosa leaving or staying in a patch after having been observed eating a particular prey species.

<u>Patch</u>	<u>First Survey</u>	<u>Second Survey</u>		<u>χ^2</u>	<u>P 0.05</u>
		<u>Stayed</u>	<u>Left</u>		
A	<u>E. modestus</u> eater	152	87	4.97	significant
	<u>B. amphitrite</u> eater	71	21		

TABLE 26 (cont

<u>Patch</u>	<u>First Survey</u>	<u>Second Survey</u>		<u>χ^2</u>	<u>P 0.05</u>
		<u>Stayed</u>	<u>Left</u>		
B	<u>E. modestus</u> eater	129	121	1.92	n.s.
	<u>B. amphitrite</u> eater	23	12		
C	<u>E. modestus</u> eater	105	129	0.0002	n.s.
	<u>B. amphitrite</u> eater	41	49		

The results show that only in A patch is there a significant difference in emigration rate between the two feeding classifications at 5% level of significance. An examination of figure 30 shows that there is a steady decline in the number of B. amphitrite prior to November 1975 followed by a rise. To ascertain the likelihood of emigration of B. amphitrite eaters causing this decline in B. amphitrite feeding by the population as a whole the results for this period are shown in Table 27 and recalculated.

TABLE 27. Number of B. amphitrite and E. modestus feeding whelks recorded as having stayed or left A patch at the following survey between February and November.

	<u>Stayed</u>	<u>Left</u>
<u>E. modestus</u> feeders	115	60
<u>B. amphitrite</u> feeders	60	16

The resulting χ^2 value is 3.79 which just fails to be significant at the 5% level of significance. An examination of the readings in Table 27 however indicates that the rate of E. modestus feeders emigrating was higher. This is the opposite trend to that required to generate whelk feeding choices which are compatible with the direction of prey availability changes.

The percentage of B. amphitrite in B patch remained fairly constant throughout the surveys and there were no great changes in whelk prey selection. It would be unlikely that a difference in emigration rates would be observed here unless there were a greater than expected immigration rate of B. amphitrite feeding whelks which were unprepared to change their prey choice

or not feed.

In the case of C patch there is also close agreement between emigration rates. Nevertheless rises in the percentage of whelks eating B. amphitrite after September could balance the general decline in the percentage earlier in the year. The data were divided into two parts, for the early readings prior to September and for the later readings after September, and the χ^2 values were calculated to be 0.34 and 1.37. These values are not significant.

7.5.3 Immigration of new L. vinosa into the patches

The L. vinosa population in a patch usually had a considerable number of animals which were not in the patch at the time of the previous survey. The proportion of new L. vinosa found in each survey averaged 49.6%. The prey selection of these new arrivals contributes significantly to the L. vinosa population's prey choice as a whole and could potentially generate changes in prey choice between surveys.

In section 7.3 it was shown that the L. vinosa population in patches A and B selected prey as expected on the basis of the relative abundance of the species. The same result was obtained in the first seven surveys in C patch which were taken before the spring B. amphitrite settlement period. These results can be further analysed by separating the L. vinosa population into two categories, new arrivals and old residents, and determine if each category feeds as expected. In Table 28 the results of χ^2 tests for each category in each patch are given. The expected number of L. vinosa feeding on B. amphitrite at each survey was calculated from the proportion of B. amphitrite present. L. vinosa were considered to have a preference for B. amphitrite over E. modestus of 1.26 to 1.

TABLE 28 Number of new arrivals and residents feeding on B. amphitrite compared with the expected number on the basis of B. amphitrite abundance if $C = 1.26$ in each patch.

<u>Patch</u>	<u>L. vinosa</u>	<u>Number of Observations</u>	<u>D.F.</u>	<u>χ^2</u>	<u>P 0.05</u>
A	Residents	12	11	10.3	n.s.
	New Arrivals	12	11	19.04	n.s.
B	Residents	12	11	12.8	n.s.
	New Arrivals	12	11	4.5	n.s.
C	Residents	7	6	3.75	n.s.
	New Arrivals	7	6	5.6	n.s.

The results indicate that both the new arrivals and the residents feed as expected. This indicates that the prey selection of the new arrivals does not in itself generate the change in the L. vinosa population's food choice. The new arrivals are sensitive to the relative abundance of the prey species at the time of their first inclusion in survey results.

7.5.4 Possibility of different feeding rates causing discrepancies in apparent prey selection.

Lower predation on the less abundant species could be caused by L. vinosa feeding on that species eating less frequently as the abundance decreases. In Table 29 the number of B. amphitrite and E. modestus eaters which are eating and not eating in subsequent surveys are compared using 2x2 contingency tables.

TABLE 29 Comparison of the likelihood of L. vinosa being found eating or not eating depending on its previous prey choice.

<u>Patch</u>	<u>Previous prey choice</u>	<u>Eating</u>	<u>Not eating</u>	<u>χ^2</u>	<u>P 0.05</u>
A	<u>E. modestus</u>	83	87	0.036	n.s.
	<u>B. amphitrite</u>	33	38		
B	<u>E. modestus</u>	146	83	0.002	n.s.
	<u>B. amphitrite</u>	14	9		

Table 29 cont.

<u>Patch</u>	<u>Previous prey choice</u>	<u>Eating</u>	<u>Not eating</u>	χ^2	<u>P</u>	<u>0.05</u>
C	<u>E. modestus</u>	54	51	0.016	n.s.	
	<u>B. amphitrite</u>	20	21			

The results indicate that there is no difference in the feeding rates of L. vinosa which are B. amphitrite eaters and those which are E. modestus eaters.

7.6 Discussion

The results of the field surveys of prey selection by L. vinosa in pneumatophore patches indicate that the relative and absolute densities of the prey species are interacting factors. At moderate prey densities the L. vinosa population is sensitive to changes in the relative abundance of the two prey species. This result was obtained from patches in which the B. amphitrite density was less than 25 per metre of pneumatophore and is typical of those patches usually found in the preferred L. vinosa foraging zone of mangroves.

Conversely it appears that if the B. amphitrite density is very high then the whelks are insensitive to changes in relative abundance and feed on the preferred species. This is the typical situation in the seaward pneumatophore fringe zone, particularly following B. amphitrite settlements when the density is in the range 50 to 170 per metre of pneumatophore.

These conclusions are to some extent compatible with the predictions a number of authors have made on the basis of optimal foraging theory. An increase in the abundance of the preferred food type is predicted to result in increasing selectivity by the predator which eventually results in all food items of lower rank being dropped from the diet. (Emlen 1966, MacArthur and Pianka 1966, Schoener 1971, Pyke, Pulliam and Charnov 1977). Whether or not a prey type is eaten is independent of its own abundance and depends only on the abundance of prey of higher rank (Pulliam 1974, Krebs 1977).

The results presented in this chapter support the first prediction

that increasing food abundance results in increasing selectivity but do not support the second prediction that the abundance of the less preferred prey is always unimportant. In optimal foraging theory a predator accepts prey of lower rank when food abundance is low because it may boost the predator's average rate of intake in this situation (Krebs 1977). The results given in section 7.4 indicate that relative abundance could be important over a density range. This would not be produced by individual L. vinosa eating each prey as encountered as L. vinosa does not forage in this manner at least when it is feeding at its normal rate in pneumatophore patches. L. vinosa were only observed eating each barnacle as encountered, irrespective of species, in experiments in which it had been starved for more than three months.

The literature contains a number of reports of marine invertebrates feeding selectively on the preferred prey species when its abundance is high. The gastropod Nucella lapillus feeds exclusively on Mytilus when it is abundant and completely ignores the less preferred barnacle species (Moore 1936 and Hancock 1960). Some starfish have been reported to feed selectively when the prey species are very abundant. Examples in the literature include the seastars Pisaster (Landenberger 1968 and Paine 1976), Astropecten irregularis (Christensen 1970) and Acanthaster planci (Moore 1978). All these reports are based on subjective impressions and no quantified measurements of density are given.

Landenberger (1968) has attempted to assess the effect of the relative and absolute density of two prey species on the feeding behaviour of Pisaster in the laboratory. He found that "the percentage of the preferred prey in the diet depends, in general, on its absolute density, and not on the relative abundance of alternatives." His experiments consisted of feeding starfish two ratios of mussels and snails at two prey densities which he classified as "low" and "high" densities.

Unfortunately restraints placed on the predators natural foraging behaviour due to being confined in the artificial environment of an aquarium creates serious difficulties in this type of experiment. For a predator to respond to either relative or absolute densities of its prey it must make an assessment of the prey during a searching phase. This searching phase could be completely altered or highly modified in character in an aquarium. If behavioural thresholds for the predator exist in the field so that there are critical prey densities above which changes in feeding behaviour are "triggered" then a laboratory experiment would be wholly inadequate. A meaningful laboratory experiment would need to follow a field assessment.

Menge (1974) has provided an example of the difference that laboratory conditions can make on the searching behaviour and subsequent prey selection of Acanthina. This whelk is time limited and can only search for prey during low risk periods in the tidal cycle. If it cannot find a preferred prey in a given time it chooses a less preferred prey rather than return to the safety of a crevice or continue foraging. In the laboratory, however, feeding was continuous and the acceptance of a less preferred prey after a period of time did not occur.

A number of authors have claimed that the relative abundance of prey species is important in determining the predator's diet. Wood (1968) examined the effect of the relative abundance of mussels and barnacles on the feeding of Urosalpinx in the field. He found no significant difference between observed attack rate on the two species and the expected attack rate on the basis of the relative number of each species available. His results consist of an examination of six quadrats, surveyed at the same time, with no information on absolute density. He concludes that attacks upon a specific prey in mixed prey habitats is a function of the relative density of the prey.

Menge (1976) examined the diet composition of Thais in three years at five different localities and found variation in the numbers of mussels and barnacles being consumed between both years and localities. He concluded that the changes in diet are positively correlated to the changes in prey abundance.

Paine (1963) found that the frequency of gastropods in the diet of Pleuroploca was closely related to the relative abundance of each species. The predator was found to exhibit little selection between gastropod prey.

Christensen (1970) also found annual variations in prey composition of Astropecten irregularis and attributes this to variation in settlement of prey. This predator feeds on newly settled invertebrates but retains its preference for certain species if they are available.

Pisaster ochraceus has been reported to feed more or less in proportion to the abundance and availability of certain prey while others are not fed upon proportionally (Feder 1959). Conversely Mauzey et al. (1968) has suggested that many sea stars feed on a variety of prey determined largely by relative abundance of the prey species although some others do not and are specialists. It must be concluded that whether a predator feeds in proportion to a particular prey must be determined for each predator and each of its prey.

The field studies of Fischer-Piette (1935) and Morgan (1972) produced a different result ^{from} that obtained in this chapter. Fischer-Piette studied the feeding of Purpura lapillus on barnacles and the mussel Mytilus edulis between 1925 and 1934 on a rocky shore. The whelk ate barnacles exclusively before 1929 when Mytilus began to spread over the rocks and kill the barnacles and it was a further two years before the whelks began to feed on the mussels. The whelks appeared not to have been able to attack Mytilus at first because it required a different technique to killing barnacles which had to be learned. Once adapted to attacking mussels they preferred them to barnacles and the whelk population increased

numerically. The predation of Purpura on Mytilus destabilised the mussel clumps and they detached leaving bare rock on which barnacles settled returning the shoreline in 1934 to the condition it was in 1925. After six months the whelks were again feeding on barnacles.

The study of Nucella feeding on the cockle Cerastoderma by Morgan (1972) has some similarity to Fischer-Piette's study as the predator also adjusted its attack and searching behaviour to a newly dominant prey type. In this case the previous dominant prey, Balanus balanoides, was eliminated by a severe winter in 1963. Morgan followed the re-establishment of the barnacles in 1965 and their subsequent spread and found behavioural differences between the whelks feeding on the two prey types.

There are two basic differences between these studies and that reported in this chapter. Firstly the difference in the relative and absolute abundance of the prey species was not nearly as great in this study and the less abundant species was never rare. Secondly in the case of L. vinosa feeding on two barnacles species the attack and searching behaviour is identical. The delay in changing from one type of prey to the other due to having to learn a new technique is not found. Other authors have reported that whelks naive to a new type of prey have difficulty at first in handling and attacking it (Orton 1929, Wood 1968).

A second important conclusion which can be drawn from the results is that there are two principal mechanisms which adjust the predator population's feeding to prey availability as it changes. Firstly there is evidence from two patches to suggest that L. vinosa which are feeding on the more abundant species are more likely to continue to feed on this species than other L. vinosa are to select it. This indicates that L. vinosa are selective in favour of the more abundant species if they have previously eaten it. An increase in the abundance of a species would therefore be followed by an increasing number of whelks becoming trained to it. Wood (1968) has demonstrated that gastropods can become trained to a prey species by "ingestive conditioning."

Secondly, new whelks entering the patch, and they often constitute half the patch population, are sensitive to and feed in proportion to the

prey abundance. This may be largely due to the success of a prey species in a patch being reflected over a large area of the mangrove in which the immigrants have been foraging. Differential immigration and emigration rates may only be important if the prey abundance in a particular patch is atypical of the area as a whole. Other possible mechanisms for changing the whelks predation on the prey species were less important although "ingestive conditioning" (Wood 1968) to the more abundant species could result in heavy predation being maintained on this species.

There is no evidence in the results to suggest that there are two genetically fixed feeding morphs in the whelk population. This supports the view of Wood (1968) and Morgan (1972) that genetic traits are not important. A polymorphism hypothesis in which the population consists of individuals which specialise on one particular species although the population as a whole feeds on a wide range of species has been suggested by Menge (1974). Direct evidence against this hypothesis being applied to L. vinosa is given in section 8.2.2.1.

If "switching" as defined by Murdoch (1969) takes place in the field then the results indicate that it is only possible in a certain density range of the preferred prey. This density range is however typical of what is found in the preferred foraging zone of the predator. The results in general fail to show a statistically significant deviation from proportional feeding. It must however be concluded that the results are not incompatible with "switching" as the whelk population can be influenced in its prey selection by relative abundances of prey, whelks feeding on the less abundant prey do change to the more abundant prey and as there is some evidence of "ingestive conditioning" to more abundant prey.

It could not be expected that strong evidence would be obtained for "switching" by the survey approach which is used in this chapter. There was no control of density or manipulation of the abundance of prey by the

experimenter and these factors varied due to natural mortality and settlement seasons. The general decline in the abundance of B. amphitrite was unfortunate as its relative abundance became too small to enable a statistical test for switching to be made. The spring settlement of B. amphitrite was not heavy enough in 1975 to raise the relative abundance of this prey above the expected mid point of a sigmoid curve. Preliminary surveys in 1974 indicated a strong "switch" to B. amphitrite with a lag in reaction time following a re-emergence of E. modestus as the more abundant prey. Finally the experimenter had no control of prey size which varied throughout the surveys for each species.

The results however can be used as a basis to design controlled field cage experiments in which the switching hypothesis can be realistically examined.

CHAPTER 8

Preliminary Laboratory experiments on switching.

8.1 Introduction

Murdoch (1969) examined switching in the laboratory using sea-shore snails as predators and combinations of mussels and barnacles as prey. He concluded that switching did not occur under most circumstances. It only occurred when the predator had a weak but variable preference for one of two prey at equality. The predator must also have a chance to become trained to whichever species was most abundant.

In this chapter experiments which investigate the possibility of finding switching for L. vinosa using various combinations of barnacle species and herbivorous gastropods as prey are reported. These experiments are essentially a preliminary investigation of the suitability of using L. vinosa and its prey to test Murdoch's switching hypothesis in the field. The experiments are therefore more limited in scope than those reported in Chapter 9. Nevertheless they provide a direct comparison of L. vinosa's feeding behaviour with those reported by Murdoch for Acanthina spirata and Thais emarginata.

8.2. Experiments on switching using barnacles as prey.

8.2.1 Methods

Barnacles are the principle food of L. vinosa and other types of prey are rarely attacked. Two species, B. amphitrite and E. modestus, are found together in pneumatophore patches. The possibility of finding a switching response for L. vinosa attacking these two species was investigated. The techniques used by Murdoch (1969) were followed as closely as possible.

Living barnacles were carefully removed from pneumatophores using a knife. Care was taken not to damage the base of the barnacles. E. modestus has a fragile membranous base and a small section of pneumatophore under the barnacles had to be removed with the barnacle

to prevent damage. The barnacles were then glued, using aquarium glue, to the bottom of plastic containers. The glue was allowed to dry overnight and the containers with attached barnacles were immersed the following morning.

The plastic containers were 10.5cm in diameter at the base, 4.5cm high and 12cm in diameter at the top. The top was covered with flyscreen wire, Cyclone fibreglass insect screening, which was stapled to the container. This prevented the whelks escaping and enabled the top to be easily removed and replaced during the observations. Holes, too small for the whelks to escape through, were punctured into the walls of the containers to improve water flow.

Two whelks and a total of 36 barnacles were placed in each container. The whelks were all adults and approximately 1.8cm in length. The barnacles were all approximately 3 to 4mm in carino-rostral diameter. This prevented size preference influencing the results.

The whelks were transferred to new containers each week. A complete change of prey was required to maintain the prey density and to prevent a deterioration in prey quality. In general the barnacles survived well for one week, but E. modestus tended to show significant mortality during the second week. The lower life expectancy of E. modestus in aquaria may have caused a decline in its attractiveness to whelks during the week it was exposed to predation. Barnacle mortality due to predation could be distinguished from other causes as the whelks leave drill holes in the opercular valves.

The plastic containers were completely immersed in well-aerated aquaria. The water in the aquaria was changed every week.

A total of nine ~~treatments~~, each using six replicates of two whelks, were done. The whelks were tested at the ratios of 6 B. amphitrite to 30 E. modestus, 18 B. amphitrite to 18 E. modestus and 30 B. amphitrite to 6 E. modestus. The whelks were trained for 65 days by placing them in aquaria with an oversupply of barnacles of one species. Control animals

were kept for the same period in aquaria without food. Thus three training regimens were obtained and tested for three prey ratios.

Prior to training the whelks were marked according to the prey they were attacking when collected in the field. The two whelks used in each container had the same previous feeding history in the field. In most cases three of the six replicates were feeding on each prey species in the field when collected. This enabled the influence of prey preference in the field prior to training to be assessed. No whelk mortality occurred in the six weeks that the experiments were taking place.

The length of time required for training was estimated by sampling the prey choice of whelks which were being fed pure diets. The whelks were removed at intervals of 14, 28, 64 days. The whelks used in this experiment were collected from nearly pure B. amphitrite patches. They showed a strong preference for B. amphitrite, 92.5% preferred B. amphitrite to E. modestus when offered equal numbers of each species before training. Eight whelks were used in each sample and their diet was scored over a period of a week. These whelks were not used in the switching experiments.

8.2.2 Results

8.2.2.1. Training effect

The effects of the duration of training on the selection of B. amphitrite in the diet is shown in figure 40. The whelks had a strong preference initially for B. amphitrite as they were feeding in a B. amphitrite patch when collected. A period of nine weeks appears to be necessary to reduce this preference significantly. The converse experiment using whelks which were feeding exclusively on E. modestus in the field was not done. E. modestus is the less preferred prey and a shorter time should be required to reduce any field conditioning before the experiments were commenced.

Whelks used in the switching experiments were collected from patches with both species of barnacles present. In Table 30 the results obtained in the nine treatments for whelks which were feeding on each prey species

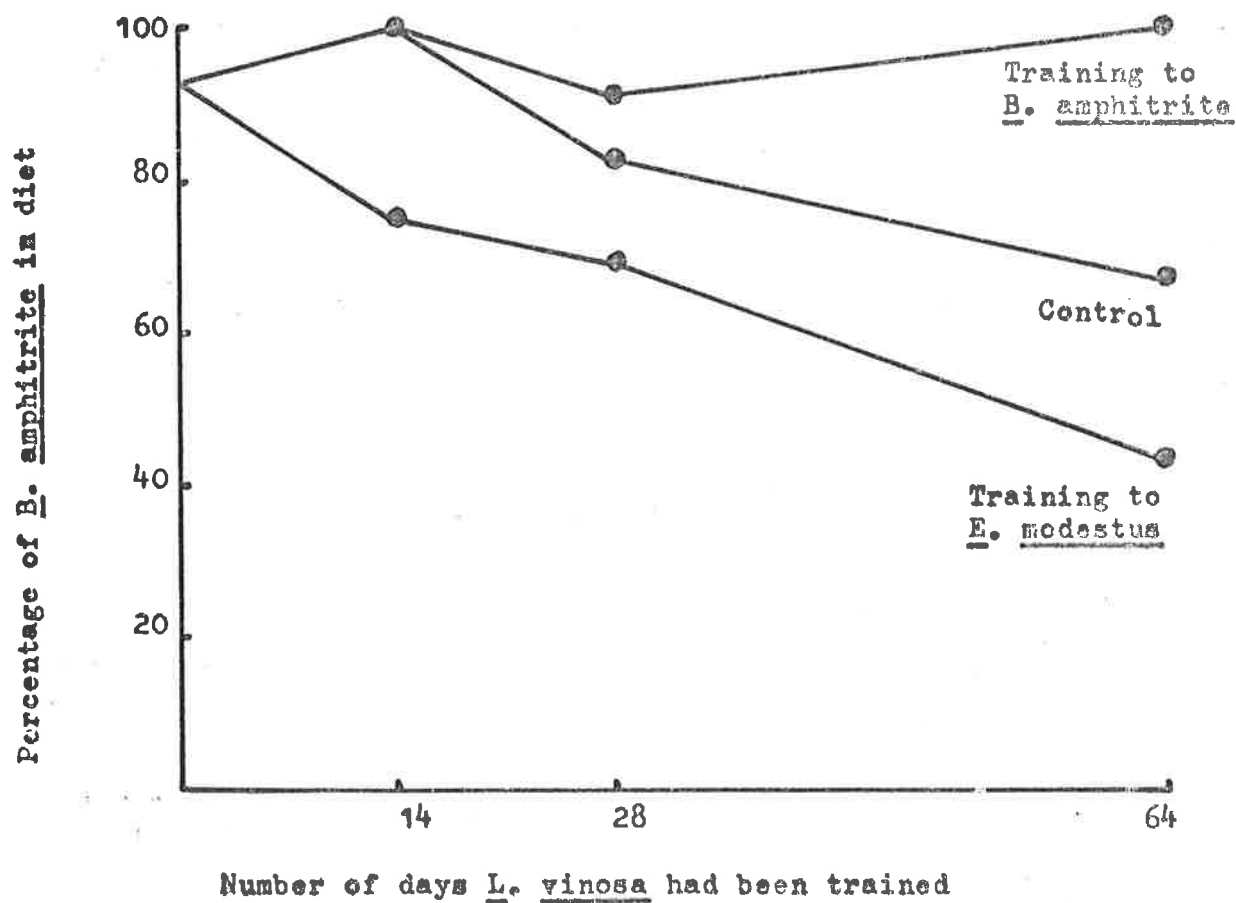


Figure 40. Effect of training on the percentage of B. amphitrite attacked when L. vinosa were presented with equal numbers of both prey species. Prior to training the whelks were feeding in almost pure B. amphitrite patches.

in the field are compared using 2x2 contingency tables. There is no significant difference between the results obtained for the two groups in each treatment. This indicates that the training period was sufficient to overcome the effects of the prior feeding history in the field. It also indicates that there are no feeding morphs or specialised feeders for either species of prey.

TABLE 30. Influence on prey selection of the whelk's feeding history in the field prior to training.

Ratio <u>B. amphitrite</u> to <u>E. modestus</u> presented to whelks	Species attacked in field prior to training	Training regimen	<u>B. amphitrite</u> attacked	<u>E. modestus</u> attacked	χ^2 (2x2 contingency table).
5 : 1	<u>B. amphitrite</u>	<u>B. amphitrite</u>	60	0	
	<u>E. modestus</u>		15	0	n.s.
	<u>B. amphitrite</u>	Control	26	1	0.23 n.s.
	<u>E. modestus</u>		43	5	
	<u>B. amphitrite</u>	<u>E. modestus</u>	30	6	0.10 n.s.
	<u>E. modestus</u>		37	7	
1 : 1	<u>B. amphitrite</u>	<u>B. amphitrite</u>	7	0	P = 0.33
	<u>E. modestus</u>		26	4	
	<u>B. amphitrite</u>	Control	30	26	0.18 n.s.
	<u>E. modestus</u>		9	5	
	<u>B. amphitrite</u>	<u>E. modestus</u>	13	13	0.02 n.s.
	<u>E. modestus</u>		14	13	

TABLE 30 (cont)

Ratio <u>B. amphitrite</u> to <u>E. modestus</u> presented to whelks	Species attacked in field prior to training.	Training regimen	<u>B. amphitrite</u> attacked	<u>E. modestus</u> attacked	χ^2 (2x2 contingency table).
1 : 5	<u>B. amphitrite</u>	<u>B. amphitrite</u>	13	12	0.14 n.s.
	<u>E. modestus</u>		7	10	
	<u>B. amphitrite</u>	Control	9	22	0.13 n.s.
	<u>E. modestus</u>		11	19	
	<u>B. amphitrite</u>	<u>E. modestus</u>	1	24	P = .5 n.s.
	<u>E. modestus</u>		1	31	

8.2.2.2 Switching experiments

The experiments which examine switching are shown in Table 31. The percentages of B. amphitrite attacked in each of the nine treatments are listed in Table 32. Treatments (1), (5) and (9), in Table 31, indicate a clear switch in terms of Murdoch's (1969) model. The individual results for each pair of whelks in these treatments are plotted in figure 41. The mean of the values for the six replicates in each treatment is also shown. A sigmoid curve could be drawn through these values.

On the basis of the results in treatment (5) the C value is calculated to be 1.26. This indicates a weak preference for B. amphitrite. There is a consistent central tendency between the replicates at equality. The percentage of B. amphitrite in the diet when the two prey are equally abundant ranges from 47% to 67.7%.

Treatments (3), (5) and (7) do not indicate reverse switching. The results for the E. modestus trained whelks, treatment (3), indicate proportional feeding when B. amphitrite is the more abundant prey. This indicates that the effect of training to the less preferred prey is not as strong as that to the more preferred prey. Treatments (4) and (6), where prey are equally abundant, support this conclusion.

TABLE 31. Number of barnacles attacked over six weeks by pairs of L. vinosa. There are six replicates for each treatment. Prior training consisted of feeding pure diets on one species for 65 days.

Ratio <u>B. amphitrite</u> to <u>E. modestus</u>	<u>Trained to B. amphitrite</u>		<u>Control</u>		<u>Trained to E. modestus</u>	
	<u>Number consumed</u>		<u>Number consumed</u>		<u>Number consumed</u>	
Number given per week	<u>B. amphitrite</u>	<u>E. modestus</u>	<u>B. amphitrite</u>	<u>E. modestus</u>	<u>B. amphitrite</u>	<u>E. modestus</u>
30 : 6	(1)		(2)		(3)	
	12	0	11	0	9	1
	15	0	13	1	7	2
	12	0	13	2	10	2
	14	0	12	1	14	4
	13	0	18	2	7	1
	<u>15</u>	<u>0</u>	<u>2</u>	<u>0</u>	<u>20</u>	<u>3</u>
	81	0	69	6	67	13
18 : 18	(4)		(5)		(6)	
	12	3	7	5	2	7
	7	0	1	1	6	5
	1	0	6	4	8	3
	0	0	9	8	1	4

Table 31 (cont)

Ratio <u>B. amphitrite</u> to <u>E. modestus</u>	<u>Trained to B. amphitrite</u>		<u>Control</u>		<u>Trained to E. modestus</u>	
	<u>Number consumed</u>		<u>Number consumed</u>		<u>Number consumed</u>	
Number given per week	<u>B. amphitrite</u>	<u>E. modestus</u>	<u>B. amphitrite</u>	<u>E. modestus</u>	<u>B. amphitrite</u>	<u>E. modestus</u>
18 :18	(4)		(5)		(6)	
	8	1	8	9	5	1
	<u>6</u>	<u>1</u>	<u>8</u>	<u>4</u>	<u>5</u>	<u>6</u>
	34	5	39	31	27	16
6 :30	(7)		(8)		(9)	
	5	3	6	4	1	9
	1	5	3	6	1	10
	5	3	4	4	0	18
	2	7	1	12	0	13
	7	4	4	9	0	5
	<u>0</u>	<u>0</u>	<u>2</u>	<u>6</u>	<u>0</u>	<u>10</u>
	20	22	20	41	2	65

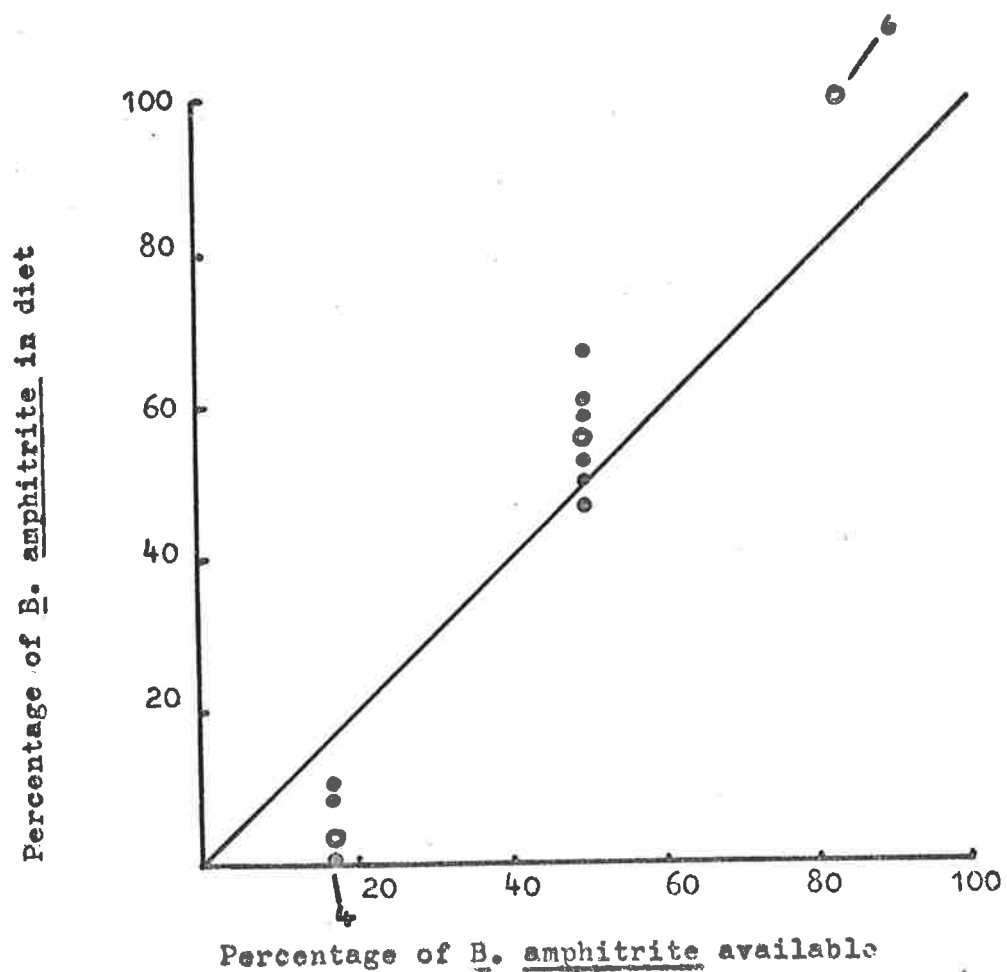


Figure 41. The observed and mean percentages of B. amphitrite in the diets of pairs of L. vinosa. Those tested at 16.7% were trained to E. modestus, those at 83.3% to B. amphitrite and those at 50% were the control animals.

TABLE 32. The percentage of B. amphitrite in the diets of L. vinosa in nine treatments. Treatment numbers correspond with those in table 31.

Treatment Number	Feeding regimen	Prey ratio offered		Percentage attacking
		<u>B. amphitrite</u>	<u>E. modestus</u>	<u>B. amphitrite</u>
1	<u>B. amphitrite</u>	30	6	100
2	Control	30	6	92
3	<u>E. modestus</u>	30	6	83.75
4	<u>B. amphitrite</u>	18	18	87.2
5	Control	18	18	55.7
6	<u>E. modestus</u>	18	18	33.75
7	<u>B. amphitrite</u>	6	30	47.6
8	Control	6	30	32.8
9	<u>E. modestus</u>	6	30	2.9

8.3 Training to herbivorous gastropods

8.3.1. Methods

L. vinosa were placed in aquaria with large numbers of either Austrocochlea or Bembicium. The whelks were left to feed for 16 weeks on only one species. Whelks in an aquarium without any prey were used as controls.

The choice experiments were done in a series of aerated plastic containers. The containers were 19.5cm in diameter and filled to a depth of 15cm with seawater. The seawater was changed every second day. Barnacles were glued to glass slides which were placed on the bottoms of the containers. Four whelks and twenty prey were placed in each container. Prey were replaced immediately after they were consumed.



8.3.2 Results

The results for experiments in which various combinations of barnacles and herbivorous gastropods were presented to whelks of different training regimens are listed in Table 33. L. vinosa has a very strong preference for barnacles when offered a choice between equal numbers of barnacles and gastropods. In neither the control nor gastropod feeding regimen experiments were any gastropods attacked. This indicates that no training to either species of gastropod occurred over the 16 weeks period that the whelks were fed pure diets.

There is a preference for Bembicium over Austrocochlea although very few of both species were attacked. Bembicium is easier to attack in aquaria and this is probably the cause of the preference. Austrocochlea is a large and comparatively strong gastropod which is capable of dislodging an attacking whelk. The whelks are repeatedly knocked against solid objects by Austrocochlea which uses a strong rotatory action. In the field attacks on Bembicium were never observed. It can avoid L. vinosa by simply climbing higher in the intertidal. Attacks on Austrocochlea in the field were observed, particularly during periods of barnacle scarcity.

The feeding rates of L. vinosa on Austrocochlea, Bembicium and barnacles are shown in Table 34. The feeding rate on gastropods is very low compared to barnacles. The higher rate of consumption of Bembicium compared to Austrocochlea is probably due to the number of unsuccessful attacks made on Austrocochlea. The shell of Bembicium is thicker, but once the snail is attacked it cannot escape. L. vinosa attack both species by drilling through the shell.

TABLE 33. Experiments on training L. vinosa to herbivorous gastropods.
Period of training was 16 weeks.

Feeding regimen	Number of whelks	Prey presented	Prey consumed or attacked in 14 days	Conclusions
<u>Austrocochlea</u>	20	<u>B. amphitrite</u> to <u>Austrocochlea</u> 1 : 1	<u>B. amphitrite</u> to <u>Austrocochlea</u> 60 0	No training occurred
<u>Bembicium</u>	16	<u>B. amphitrite</u> to <u>Bembicium</u> 1 : 1	<u>B. amphitrite</u> to <u>Bembicium</u> 13 0	No training occurred
Control	20	<u>B. amphitrite</u> to <u>Austrocochlea</u> 1 : 1	<u>B. amphitrite</u> to <u>Austrocochlea</u> 56 0	Strong preference for barnacles
Control	16	<u>B. amphitrite</u> to <u>Bembicium</u> 1 : 1	<u>B. amphitrite</u> to <u>Bembicium</u> 15 0	Strong preference for barnacles
Control	16	<u>Bembicium</u> to <u>Austrocochlea</u> 1 : 1	<u>Bembicium</u> to <u>Austrocochlea</u> 6 3	<u>Bembicium</u> preferred

TABLE 34. Feeding rates of L. vinosa when presented with an oversupply of prey in aquaria.

Prey	Prey consumed per whelk per week
Barnacles	1.55
<u>Austrocochlea</u>	0.17
<u>Bembicium</u>	0.26

8.4 Discussion

The results indicate that in the laboratory L. vinosa shows switching with respect to its two barnacle prey species. Preference at equality was weak and the C value was calculated to be 1.26. L. vinosa could be trained to either species by feeding it a pure diet of that species.

There is however a lack of variability between replicates when equal numbers of prey are available. This result is not compatible with the generalisations which have been made by Murdoch (1969) on the behaviour of a switching predator. The combined results from this laboratory study and the field experiments relevant to this point will be discussed in section 9.4.

The feeding response of L. vinosa to its two prey species is not symmetrical. E. modestus trained whelks accept B. amphitrite more readily than vice versa.

No training occurred when L. vinosa were fed pure diets of Austrocochlea or Bembicium. The preference for barnacles is strong and no switching is possible between barnacles and gastropods. These results are similar to the observations of Murdoch (1969) when Thais was used as a predator.

Results obtained in laboratory experiments of this type are not necessarily a good indication of whelk behaviour in the field. The confinement of pairs of whelks in small plastic containers could result in the prey choice of one whelk being influenced by the other (Murdoch and Oaten 1975). Pratt (1974) found that Urosalpinx was attracted to prey species in standing water which were not attractive in the field. The predators are also confined with an abundant supply of prey which restricts natural searching behaviour and affects the risks involved in prey rejection.

CHAPTER 9

Field cage experiments on switching

9.1 Introduction

Studies on switching using invertebrate predators have invariably been carried out under laboratory conditions. There is no evidence that an invertebrate predator switches in the field (Murdoch and Oaten 1975). In this chapter the results obtained from field cage experiments on switching are presented. These experiments were designed to examine prey selection by L. vinosa in pneumatophore patches in which the prey abundance is manipulated and controlled by the experimenter.

The primary aim of these experiments was to determine if L. vinosa switches in its natural biotic and abiotic environment. The duration of most experiments was at least eight weeks and the behaviour of the predators was quantified at fortnightly intervals. Changes in the feeding behaviour with time could therefore be detected. This is particularly useful in the reverse switching experiments where a time lag is expected (Murdoch 1969).

The technique used for quantifying the predator's feeding response provides information on feeding rates, as well as the relative frequency of attacks on each species. The results therefore provide an indication of the functional response to each prey species. There is a lack of experimental data in the literature on the relationship between switching and the functional response to each prey species (Murdoch 1973, Oaten and Murdoch 1975).

Some field cage experiments were also designed to examine the hypothesis, proposed in section 7.4.1, that the switching response is not obtained when the absolute density of the preferred prey species is too high. Switching experiments reported in the literature have not investigated this possibility. Murdoch and Oaten (1975) have however predicted the opposite trend for marine snails, that is switching at high total prey abundance.

9.2 Methods

Aspects of the feeding behaviour of L. vinosa were examined in artificial pneumatophore patches. The patches were established in field cages and were designed to be typical of those found naturally in the field. Prey density and predator feeding history were experimenter-controlled. Restraints on the movement of predators out of the patches was the only unnatural feature of the experimental design.

The cages were constructed in the field and consisted of fibreglass fly screen walls which were attached to wooden stakes at each corner. Each cage enclosed an area of one square metre. The sides of the cages were one metre long and the height was approximately 50cm. To prevent the whelks from escaping the sides of the cages extended 20cm into the soft mud and the tops of the cages were covered with flyscreen wire. The tops were attached with staples and were removed at each survey.

Pneumatophores greater than 18cm in length with numerous barnacles attached were collected. A notch was cut 18cm from the tip and barnacles were scraped off until the desired prey composition on the pneumatophore was left. The modified pneumatophores were then implanted into the mud inside the cages up to the 18cm notch. Pneumatophores are slow to wither and the predators are thus provided with a realistic simulation of a natural prey patch.

The barnacles which were left on the pneumatophores were 3 to 4mm in carino-rostral diameter. This standardisation of prey size was necessary as it removes size preferences of the predator as a factor in the experiments. Many pneumatophores had to be examined in the field for each pneumatophore that was collected. At some times of the year it was extremely difficult to find pneumatophores with prey of suitable size and this considerably limited the number of experiments which could be carried out.

The total barnacle density was standardised in each cage to 516 or 11.2 per metre of pneumatophore. The total length of pneumatophore available for searching by the whelks in each cage was 46.08 metres. This length was divided into 256 individual pneumatophores which were each 18cm in height. On the basis of the field observations described in Chapter 7, I would expect that switching would occur at this density.

Details of the experimental designs are listed in Table 35. The three parameters which vary between experiments are prey ratio, the pattern of prey distribution and the predators' prior feeding history.

Two prey distribution patterns were examined. For an unclumped, that is evenly distributed prey, design experiment there were two barnacles on each pneumatophore. The more abundant prey would be found on each pneumatophore but the less abundant prey would be found only on every third pneumatophore. Four of the 256 pneumatophores had an extra barnacle to give a total number of 516 barnacles per cage. This allows an exact 5 to 1 ratio.

In the clumped design experiments the prey were distributed between 120 pneumatophores and the remaining 136 pneumatophores had no attached barnacles. The predator thus faced a "risk" of not finding any prey on a pneumatophore. On the pneumatophores with prey they encountered five barnacles of the same species. Thus 20 pneumatophores had five prey of the less abundant species and 100 pneumatophores had 5 prey of the more abundant species.

Clumping would seem to increase the likelihood of the predator having more than one feed on the same prey species. The effect of one feed on the predators behaviour was not found to be significant. The clumped experiments were introduced to examine reverse switching, as it was considered possible that the regular occurrence of the preferred prey in the unclumped experiment could hinder retraining to the less preferred species when it was more abundant. The clumped design is more realistic as prey are most often found in groups. A proportion, normally about one in two, of the

pneumatophores in field patches have no barnacles on them.

Predators were trained in field cages by feeding them a pure diet of one species for approximately twelve weeks. An excess of prey was provided. Given a feeding rate of 1.65 prey per week the training would thus consist of approximately 20 consecutive feeds on the same species. In the control cages the whelks were given pneumatophores on which there were no barnacles. Little cannibalism was observed although the predator density was very high.

The feeding behaviour of the whelks in the experiments was quantified every two weeks. This time interval was chosen as the tidal cycle resulted in a series of low tides every second week. In some cases a 48-hour survey was undertaken to determine the immediate response of the predators.

Records were kept of the feeding activity of each whelk during the experiments. The whelks were individually numbered using nail polish. They were classified as attacking a particular prey species or not feeding.

Only those whelks which were on pneumatophores were scored. Those whelks which were escaping were returned to the cage if found on or near the cage. Fluctuations in the total number of whelks scored in each cage between surveys therefore occur.

It was not possible to assess accurately the number of prey killed per fortnight. In the field the cause of prey mortality cannot be determined as the opercular plates through which the whelks drill are lost due to water movement. Furthermore E. modestus can become detached from the pneumatophore after being attacked by the whelk. To accurately quantify prey mortality all the pneumatophores would have to be removed and replaced each fortnight. This would have been impractical.

An attempt was nevertheless made to maintain prey density.

Pneumatophores with dead barnacles were replaced, when detected, at the first two surveys in all experiments. Prey density was not rigorously maintained after the second survey. The experiment to determine the "C" value was, however, an exception and the prey density was maintained for 12 weeks.

L. vinosa do not aggregate during feeding. More than twenty whelks are seldom found in one square metre of mangrove. Unnaturally high predator densities were therefore avoided and most experiments were run with twenty predators per cage. The number of predators could be expected to consume about 12% of the prey per fortnight. Higher predator densities were used in some experiments and in these cases whelks of opposing feeding histories were used in equal numbers. This reduced predation to some extent on any one species and helped to maintain the prey ratio. Results from these experiments were similar to those in which twenty predators were used.

Table 35. Design of field cage experiments. Each cage had 256 pneumatophores which were 18cm in length. The total prey density was 516 barnacles per square metre.

Training regimen	Experiment examines	Prey distribution	Ratio <u>B.amphitrite</u> : <u>E.modestus</u>	Density of <u>B. amphitrite</u>		Density of <u>E. modestus</u>		Number Replicates	Pneumatophores with	
				per m ²	per metre Pneumatophore	per m ²	per metre Pneumatophore		<u>Balanus</u>	<u>Elminius</u>
<u>B.amphitrite</u>	Switching	Unclumped	5:1	430	9.33	86	1.87	2	256	82
<u>E. modestus</u>	Switching	Unclumped	1:5	86	1.87	430	9.33	3	82	256
		Clumped	1:5	86	1.87	430	9.33	2	20	100
<u>B.amphitrite</u>	Reverse Switching	Unclumped	1:5	86	1.87	430	9.33	3	82	256
		Clumped	1:5	86	1.87	430	9.33	2	20	100
<u>E. modestus</u>	Reverse Switching	Unclumped	5:1	430	9.33	86	1.87	2	256	82
Unfed	Value of 'C'	Unclumped	1:1	256	5.56	256	5.56	1	256	256
Unfed	Control	Unclumped	5:1	430	9.33	86	1.87	1	256	82
Unfed	Control	Clumped	1:5	86	1.87	430	9.33	1	20	100

9.3 Results

The results of the field cage experiments are presented in the following sections. The 95% confidence limits, except where otherwise stated, were calculated using Table VIII.1 in Fisher and Yates (1953) as the sample sizes are small.

9.3.1. Switching experiments

In these experiments L. vinosa are presented with a mixture of prey in which the species to which they were trained is most abundant. If L. vinosa feeds disproportionately heavily on the more abundant species, in both cases, it can be said to switch.

9.3.1.1. L. vinosa trained to B. amphitrite.

L. vinosa which were trained to B. amphitrite were presented with a mixture of B. amphitrite and E. modestus in the ratio of 5 to 1. The results obtained from two cages are shown in Table 36 and plotted in figure 42.

TABLE 36. Feeding behaviour of L. vinosa trained to B. amphitrite over a period of ten weeks. The ratio of B. amphitrite to E. modestus was 5 : 1. The prey were not clumped.

Experiment	<u>L. vinosa</u> behaviour	2	4	Weeks		10	Total
				6	8		
1	Eating <u>B. amphitrite</u>	6	6	6	5	4	27
	Eating <u>E. modestus</u>	0	3	0	0	0	3
	Not eating	11	10	10	13	13	57
2	Eating <u>B. amphitrite</u>	4	7	7	5	7	30
	Eating <u>E. modestus</u>	1	0	0	0	0	1
	Not eating	12	9	7	12	8	48
Total	Eating <u>B. amphitrite</u>	10	13	13	10	11	57
	Eating <u>E. modestus</u>	1	3	0	0	0	4
	Not eating	23	19	17	25	21	105

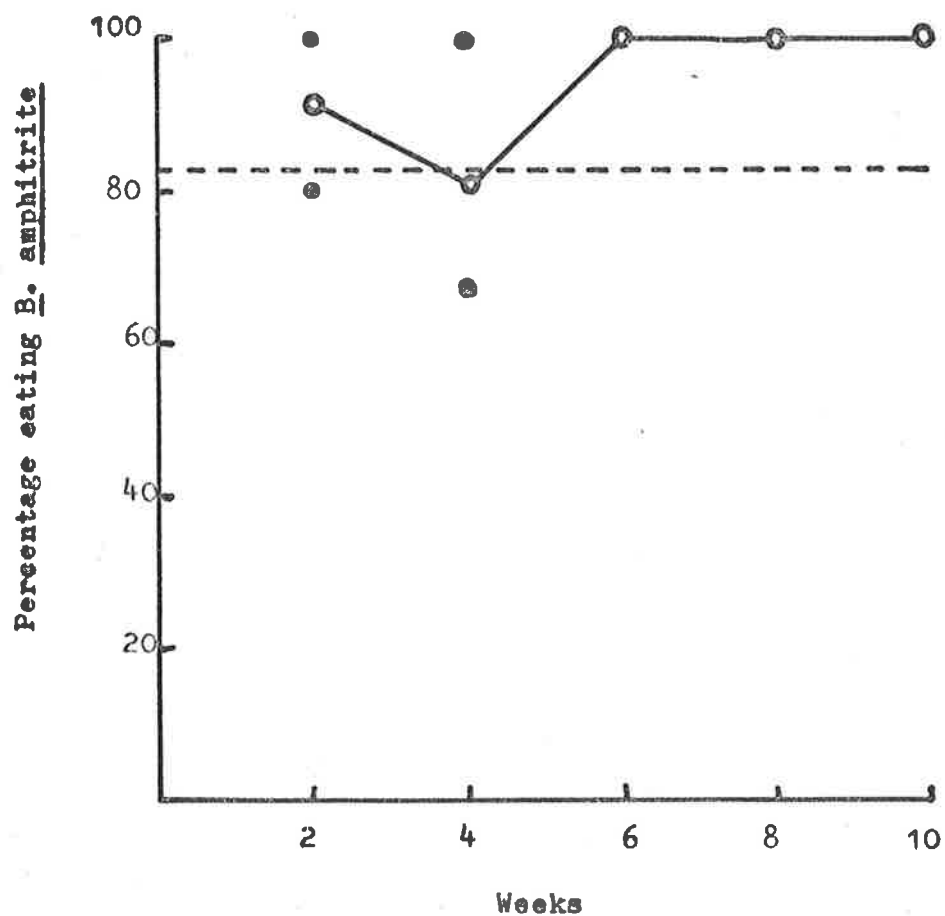


Figure 42. Percentage of *L. vinosa* trained to *B. amphitrite* eating *B. amphitrite* over a ten week period. The ratio of *B. amphitrite* to *E. modestus* was 5:1 and the prey were not clumped. The mean (●) and the results of two experiments (●) are shown.

The results indicate a switch to B. amphitrite in all but the four week reading. There is a significant difference between the first two readings and the final three readings which indicates that the switch is becoming stronger (Fisher's exact probability test, $P = 0.03$).

In the ten week period B. amphitrite constitutes 93.4% of the recorded prey. The 95% confidence limits are 83.6 to 98.2. This overlaps the expected percentage in the diet, 86.3%, if L. vinosa feeds proportionally to prey abundance and $C = 1.26$.

The individual L. vinosa were numbered and it is therefore possible to compare the first observed feed of each L. vinosa with the subsequent prey choice. The results of this analysis, given in Table 37, indicate that B. amphitrite was more likely to be eaten after the first feed (Fisher's exact probability test, $P = 0.046$).

TABLE 37. First and subsequent observed prey choices of L. vinosa in the experiment shown in Table 36. The total number of L. vinosa in each category is shown.

	First observed feed	Subsequent feeds pooled
Eating <u>B. amphitrite</u>	25	32
Eating <u>E. modestus</u>	4	0

9.3.1.2. L. vinosa trained to E. modestus.

9.3.1.2.1. Prey not clumped.

L. vinosa which were trained to E. modestus were presented with a mixture of B. amphitrite and E. modestus in the ratio of 1 to 5. The results obtained from three cages are shown in Table 38 and plotted in figure 43.

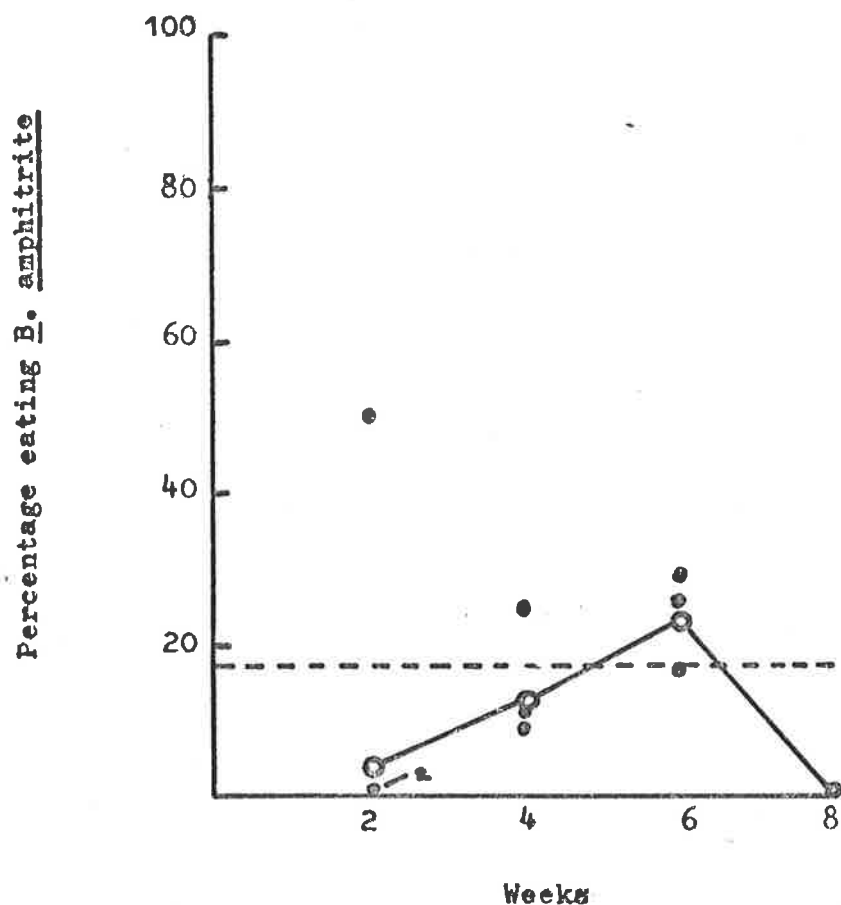


Figure 43. Percentage of *L. vinosa* trained to *E. modestus* eating *B. amphitrite* over an eight week period. The ratio of *B. amphitrite* to *E. modestus* was 1:5 and the prey were not clumped. The mean (O) and the results from three experiments (•) are shown.

TABLE 38. Feeding behaviour of L. vinosa trained to E. modestus over a period of eight weeks. The ratio of B. amphitrite to E. modestus was 1 : 5. The prey were not clumped.

Experiment	<u>L. vinosa</u> behaviour	Week				Total
		2	4	6	8	
1	Eating <u>B. amphitrite</u>	0	1	2	0	3
	Eating <u>E. modestus</u>	7	3	5	2	17
	Not eating	6	10	9	16	41
2	Eating <u>B. amphitrite</u>	0	1	1	0	2
	Eating <u>E. modestus</u>	8	8	5	2	23
	Not eating	7	10	14	14	45
3	Eating <u>B. amphitrite</u>	1	1	1	0	3
	Eating <u>E. modestus</u>	1	7	3	4	15
	Not eating	9	7	12	11	39
Totals:	Eating <u>B. amphitrite</u>	1	3	4	0	8
	Eating <u>E. modestus</u>	16	18	13	8	55
	Not eating	22	35	35	41	125

The percentage of B. amphitrite in the diet was 12.7% which is less than the expected percentage, 20.2, if L. vinosa fed proportionally with $C = 1.26$. The 95% confidence limits are 5.6 to 24.7. This overlaps the expected percentage for proportional feeding and thus while the results are consistent with switching they fail to eliminate the alternative hypothesis of proportional feeding.

There is no apparent time trend over the eight week period in figure 43. The combined two and four week readings are not significantly different from the combined six and eight week readings (Fisher's exact probability test, $P = 0.24$). The results for the first observed feed and subsequent feeds, shown in Table 39, are also not significantly different (Fisher's exact probability test, $P = 0.255$). *p=0.433*

plus more 2-4 cases

TABLE 39. First and subsequent observed prey choices of L. vinosa in the experiment shown in Table 38. The total number of L. vinosa in each category is shown.

	First observed feed	Subsequent feeds pooled
Eating <u>B. amphitrite</u>	4	4
Eating <u>E. modestus</u>	33	22

9.3.1.2.2. Prey clumped

The previous experiment was repeated with a clumped prey distribution. The results obtained from two cages are shown in Table 40 and plotted in figure 44.

TABLE 40. Feeding behaviour of L. vinosa trained to E. modestus, over a period of eight weeks. The ratio of B. amphitrite to E. modestus was 1 : 5. The prey were clumped.

Experiment	<u>L. vinosa</u> behaviour	Weeks				Total
		2	4	6	8	
1	Eating <u>B. amphitrite</u>	2	1	0	0	3
	Eating <u>E. modestus</u>	3	6	2	3	14
	Not eating	11	8	15	9	43
2	Eating <u>B. amphitrite</u>	2	0	2	1	5
	Eating <u>E. modestus</u>	9	6	5	6	26
	Not eating	9	11	11	8	39
Totals:	Eating <u>B. amphitrite</u>	4	1	2	1	8
	Eating <u>E. modestus</u>	12	12	7	9	40
	Not eating	20	19	26	17	82

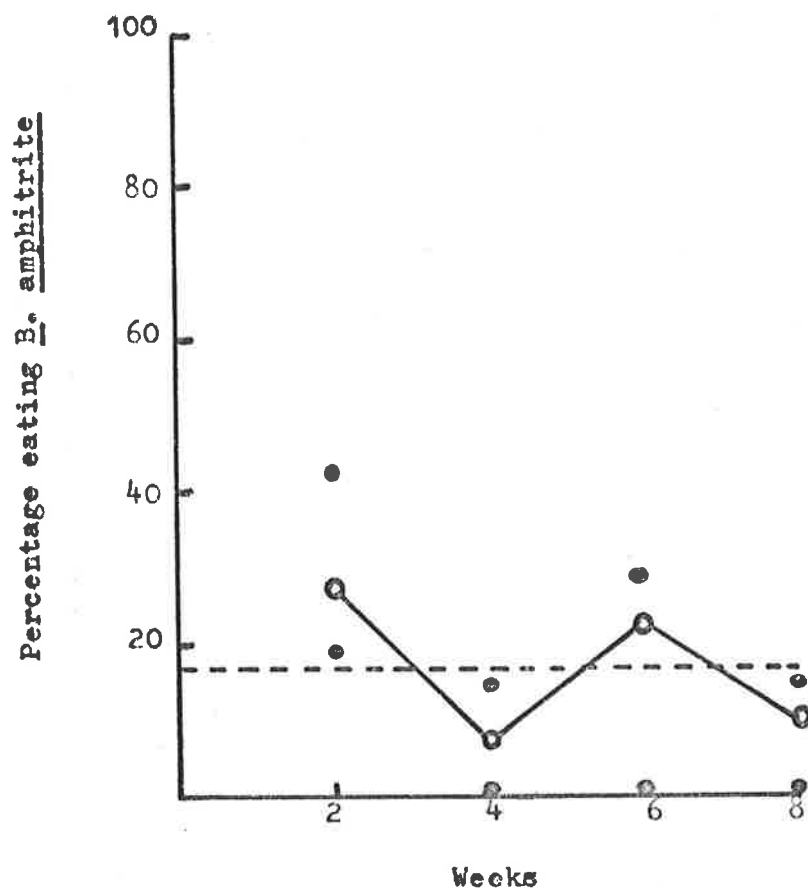


Figure 44. Percentage of *L. vinosa* trained to *E. modestus* eating *B. amphitrite* over an eight week period. The ratio of *B. amphitrite* to *E. modestus* was 1:5. The prey were clumped. The mean (O) and the results of two experiments (●) are shown.

The overall result is proportional feeding. The mean percentage of B. amphitrite in the diet is 16.3% and the 95% confidence limits are 5.5 to 34.6. This result is due to the unexpectedly high predation on B. amphitrite in both cages in the second week. If this reading were disregarded the percentage of B. amphitrite in the diet would be 12.5% which is close to ^{the} result obtained for the unclumped design experiment.

TABLE 41. First and subsequent prey choice of L. vinosa in the experiment shown in Table 40. The total number of L. vinosa in each category is shown.

	First observed feed	Subsequent feeds pooled
Eating <u>B. amphitrite</u>	7	1
Eating <u>E. modestus</u>	23	18

The percentage of B. amphitrite in the diet decreased from 23.3 to 5.3 between the first and subsequent observed feeds. The results shown in Table 41 for the first observed feed and the subsequent observed feeds are however not significantly different (Fisher's exact probability test, $P = 0.085$). The results are therefore compatible with either switching or proportional feeding.

9.3.2 Reverse switching experiments.

In these experiments L. vinosa are presented with a mixture of prey in which the species to which they were trained is less abundant. If the whelks feed disproportionately heavily on the more abundant species then they can be said to "reverse" switch. This would require retraining and a time lag could be expected before the response is shown. Unlike the switching experiments the response in this case cannot be "forced" by the whelks previous feeding history.

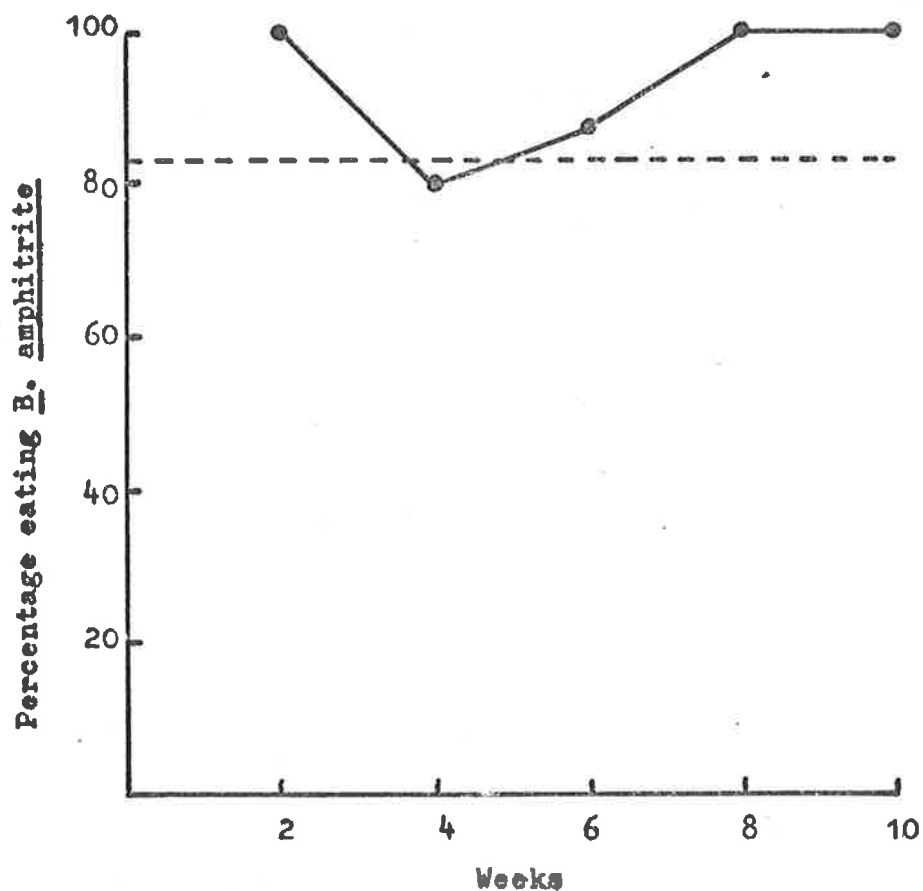


Figure 45. Percentage of L. vinosa trained to E. modestus eating B. amphitrite over a ten week period. Ratio of B. amphitrite to E. modestus was 5:1.

9.3.2.1. L. vinosa trained to E. modestus.

L. vinosa trained to E. modestus were presented with a mixture of B. amphitrite and E. modestus in a ratio of 5 to 1. The prey were not clumped. The results for two cages are shown in Table 42.

TABLE 42. Feeding behaviour of L. vinosa trained to E. modestus over a period of ten weeks. The ratio of B. amphitrite to E. modestus was 5 to 1. The prey were not clumped.

Experiment	<u>L. vinosa</u> behaviour	2	4	Weeks		10	Total
				6	8		
1	Eating <u>B. amphitrite</u>	9	4	1	4	7	25
	Eating <u>E. modestus</u>	0	3	1	0	0	4
	Not eating	7	11	15	13	11	57
2	Eating <u>B. amphitrite</u>	7	8	6	5	6	32
	Eating <u>E. modestus</u>	0	0	0	0	0	0
	Not eating	8	11	7	14	12	52
Totals	Eating <u>B. amphitrite</u>	16	12	7	9	13	57
	Eating <u>E. modestus</u>	0	3	1	0	0	4
	Not eating	15	22	22	27	23	98

B. amphitrite formed 93.4% of the diet of L. vinosa over the ten week period. The 95% confidence limits are 83.6 to 98.2. The expected proportion in the diet if L. vinosa fed proportionally with $C = 1.26$ is 86.3%. The results are therefore compatible with either reverse switching or proportional feeding.

The results for each two week period are plotted in figure 45 and there is no apparent time trend. There is no significant difference in the prey selected by L. vinosa on the first occasion they were observed feeding and the subsequent occasions (Fisher's exact probability test, $P = 0.39$).

TABLE 42(a). First and subsequent prey choice of L. vinosa in the experiment shown in Table 42. The total number of L. vinosa in each category is shown.

	First observed feed	subsequent feeds pooled
Eating <u>B. amphitrite</u>	29	28
Eating <u>E. modestus</u>	2	2

If we assume that Table 42 indicates a reverse switch, then the results indicate that L. vinosa trained to E. modestus do not require a time lag before they reverse switch to B. amphitrite and that the preference for B. amphitrite does not become stronger with time.

9.3.2.2. L. vinosa trained to B. amphitrite.

L. vinosa which had been trained to B. amphitrite were presented with a mixture of B. amphitrite and E. modestus in the ratio of 1 to 5. A series of three experiments were run in field cages. The prey were not clumped. The results are shown in Table 43 and the percentage of B. amphitrite in the diet over an eight week period is plotted in figure 46.

TABLE 43. Feeding behaviour of L. vinosa trained to B. amphitrite.
B. amphitrite and E. modestus were presented in the ratio of 1 to 5.
They were not clumped.

Experiment	<u>L. vinosa</u> behaviour	48hrs	Weeks				Total
			2	4	6	8	
1	Eating <u>B. amphitrite</u>	0	2	1	0	1	4
	Eating <u>E. modestus</u>	2	1	2	1	2	7
	Not eating	14	7	9	18	16	64
2	Eating <u>B. amphitrite</u>	1	3	1	3	0	8
	Eating <u>E. modestus</u>	0	2	3	3	3	11
	Not eating	15	11	12	9	10	57
3	Eating <u>B. amphitrite</u>	2	2	0	0	0	4
	Eating <u>E. modestus</u>	2	2	1	0	2	7
	Not eating	14	11	13	16	15	69
Totals	Eating <u>B. amphitrite</u>	3	7	2	3	1	16
	Eating <u>E. modestus</u>	4	5	6	4	7	26
	Not eating	43	29	34	43	41	190

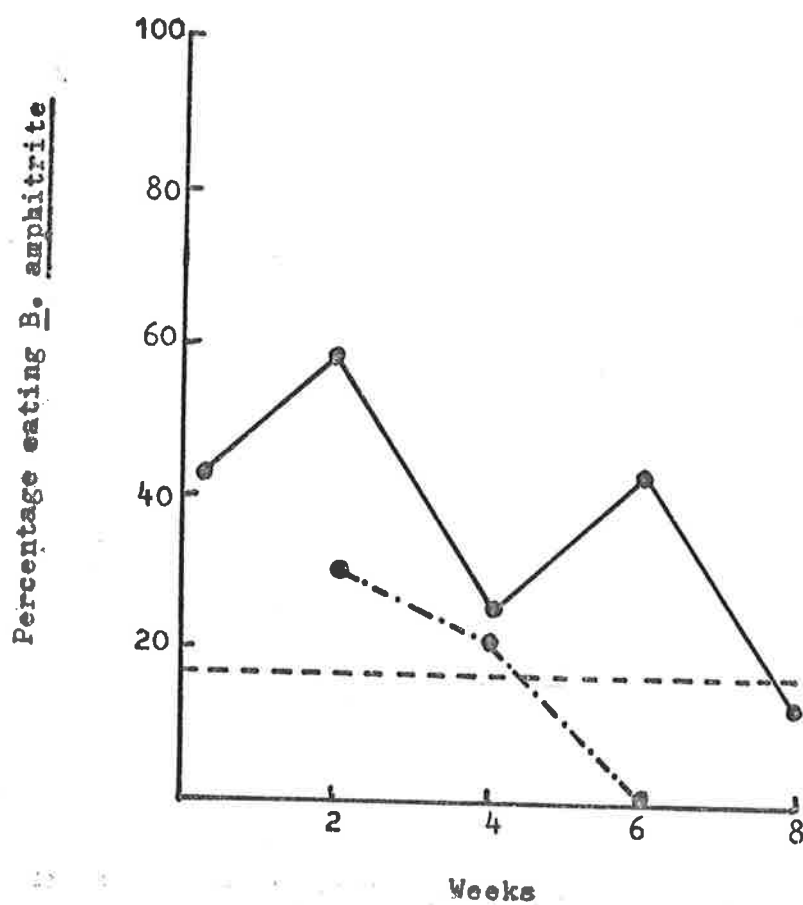


Figure 46. Percentage of L. vinosa trained to B. amphitrite eating B. amphitrite over an eight week period. The ratio of B. amphitrite to E. modestus was 1:5. Results when prey were not clumped is shown — and when clumped - - - - -.

The percentage of B. amphitrite in the diet over the eight weeks was 38.1. The 95% confidence limits are 23.4 to 54.5.

This is higher than proportional feeding, 20.2% if $C=1.26$, and the results do not therefore support either the hypothesis of reverse switching or proportional feeding.

There is however an apparent trend to lower predation on B. amphitrite. After eight weeks it was being attacked only 12.5% of the time. The 95% confidence limits are 0.3 to 52.75. This result is consistent with both reverse switching and proportional feeding.

The apparent trend is however not significant. There is no significant difference between the 48 hour and two week readings compared to the six and eight week readings ($\chi^2=1.38$, 1df, $P>0.05$). Furthermore the first observed feed of individual L. vinosa and their subsequent feeds are not significantly different ($\chi^2=0.15$, 1df, $P>0.05$).

A second series of experiments were run with a clumped design to further investigate whether reverse switching to the less preferred prey can take place in the field. The ratio and densities of the prey were the same as in the previous series. The results which were obtained from two cages are shown in Table 44. The average percentage of B. amphitrite which were attacked is plotted in figure 46.

TABLE 44. Feeding behaviour of L. vinosa trained to B. amphitrite. The ratio of B. amphitrite to E. modestus was 1 to 5. The prey were clumped.

Experiment	<u>L. vinosa</u> behaviour	Weeks				Total
		2	4	6	8	
1	Eating <u>B. amphitrite</u>	2	2	0	0	4
	Eating <u>E. modestus</u>	3	4	5	0	12
	Not eating	13	12	14	14	53
2	Eating <u>B. amphitrite</u>	1	1	0	2	4
	Eating <u>E. modestus</u>	4	7	2	1	14
	Not eating	12	7	14	11	44
Totals	Eating <u>B. amphitrite</u>	3	3	0	2	8
	Eating <u>E. modestus</u>	7	11	7	1	26
	Not eating	25	19	28	25	97

The overall proportion of B. amphitrite in the diet was 23.5%. The 95% confidence limits are 10.4 to 41.4. This result is consistent with both the hypotheses.

There is again an apparent trend to lower predation on B. amphitrite with increasing time. A comparison of the two and four week readings with the six and eight week readings however indicate that there is no significant difference (Fisher's exact probability test, $P = 0.33$). There is also no significant difference between the first observed feed of individual L. vinosa and subsequent observed feeds (Fisher's exact probability test, $P = 0.31$).

The results of the clumped and unclumped design experiments both fail to show a reverse switch to E. modestus. This could be because eight weeks is not long enough to obtain a reverse switch at the prey densities used in these experiments. The overall proportion of B. amphitrite in the diet is higher than expected in both cases. If this proportion were to decline further with time it is unclear from the results whether proportional feeding or a reverse switch would occur. Reverse switching does, however, appear more likely with clumped prey, from these data. In general a clumped distribution of prey is more often found in pneumatophore patches due to the gregarious settling behaviour of barnacles.

9.3.3. Determination of "C" value.

The ratio of prey species in the diet when equal numbers of two prey species are presented to untrained predators can be used as an operational measure of preference (Murdoch and Marks 1973). This measure of preference has been called the "C" value (Murdoch 1969).

To determine the C value for L. vinosa in the field untrained whelks were presented with equal numbers of B. amphitrite and E. modestus. The experiment was continued for twelve weeks. The prey density was maintained by replacing pneumatophores with dead barnacles on them with new pneumatophores with living barnacles on them every two weeks. The results are shown in Table 46.

TABLE 46. Feeding behaviour of L. vinosa which had been unfed for twelve weeks. The ratio of B. amphitrite to E. modestus was 1 to 1.

<u>L. vinosa</u> behaviour	48 hrs.	2	4	Weeks				Total
				6	8	10	12	
Eating <u>B. amphitrite</u>	3	6	5	3	6	2	4	29
Eating <u>E. modestus</u>	3	5	5	4	1	4	1	23
Not eating	14	9	7	9	9	5	7	60

The results indicate that B. amphitrite is preferred to E. modestus. The preference is weak and the "C" value, calculated from the totals for the twelve week period is 1.26. The 95% confidence limits for 55.8%, $n = 52$ are 41.3 to 69.6. This estimate is obtained using Table VIII₁ in Fisher and Yates (1953). The corresponding 95% confidence limits for C are 0.70 to 2.29.

Individual whelks were numbered and changes in their prey choice over the twelve week period were recorded. Twenty whelks were originally placed in the cage. Unfortunately some escaped and the number dropped in the twelve week period. The number of times individual whelks were observed feeding is summarised in Table 47.

TABLE 47. Number of times individual L. vinosa were observed feeding in the seven surveys carried out over a twelve week period.

Number of times feeding	Number of individual whelks
0	1
1	3
2	5
3	5
4	3
5	2
6	0
7	1

Predators which switch have been predicted to show weak but variable preferences at equality (Murdoch, Avery and Smyth 1975) . Whether or not individual L. vinosa specialised on one prey species is examined in Table 48. The number of L. vinosa eating successive meals of the same prey species is compared with the number which should eat the same prey species if the prey species was chosen at random at each meal.

TABLE 48. Comparison of the number of L. vinosa eating successive meals of the same prey with the number expected if L. vinosa eat at random.

<u>Number of</u> <u>times feeding</u>	<u>Number of</u> <u>L. vinosa</u> <u>observed</u>	<u>Eating same</u> <u>prey species</u> <u>each time</u> <u>observed</u>	<u>Eating diff.</u> <u>prey species.</u>	<u>Number expected</u> <u>to be eating</u> <u>same prey if</u> <u>L. vinosa eat</u> <u>at random.</u>	χ^2
2	16	8	8	8	n.s.
3	10	2	8	2.5	n.s.
4	6	0	6	0.75	n.s.

The results indicate that individual L. vinosa did not specialise on one prey species. The preference at equality was therefore consistent between individuals. If preference was variable then "runs" on one type of prey by individual whelks would have been expected.

9.3.4 Controls.

L. vinosa which were kept in cages without any prey, while those used in other experiments were being trained, were used as controls. Table 49 shows the results obtained over a period of eight weeks for the prey selection of untrained L. vinosa which were presented with B. amphitrite and E. modestus in ratio of 1 to 5.

TABLE 49. Feeding behaviour of L. vinosa which were unfed for twelve weeks. The ratio of B. amphitrite to E. modestus presented to L. vinosa was 1 to 5. The prey were clumped.

<u>L. vinosa</u> behaviour	Weeks				Total
	2	4	6	8	
Eating <u>B. amphitrite</u>	1	1	0	1	3
Eating <u>E. modestus</u>	10	8	7	3	28
Not eating	8	5	8	9	30

The proportion of L. vinosa eating B. amphitrite was 9.7%. The 95% confidence limits are 2.0 to 25.7. This result is consistent with switching but does not exclude the possibility of proportional feeding.

In Table 50 the first and second observed feeds for individual L. vinosa are shown.

TABLE 50. First and second observed prey choice of L. vinosa in the experiment shown in Table 49.

The total number of L. vinosa in each category is shown.

<u>L. vinosa</u> behaviour	First observed feed	Second same	Second different
Eating <u>B. amphitrite</u>	1	0	1
Eating <u>E. modestus</u>	15	9	1

The percentage of L. vinosa choosing B. amphitrite on their first observed feed was 6.3. The 95% confidence limits are 0.2 to 30.2. The percentage choosing B. amphitrite on the second observed feed was 9.1. The 95% confidence limits are 2.3 to 41.4. Both the readings are below the expected rate of feeding on B. amphitrite and consistent with switching. The 95% confidence limits are however very wide due to the small sample sizes and the possibility of proportional feeding cannot be excluded.

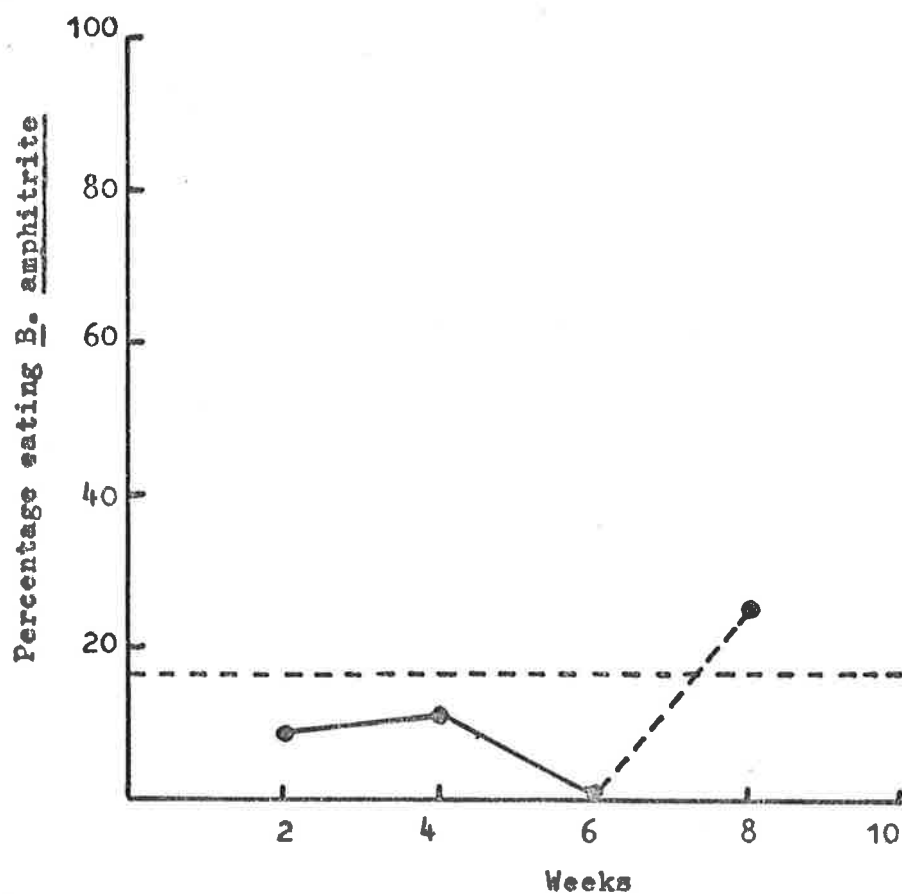


Figure 47. Percentage of *L. vinosa* eating *B. amphitrite* when the ratio of *B. amphitrite* to *E. modestus* was 1:5.

L. vinosa were not fed for 12 weeks prior to the experiment.

Prey were clumped.

The results obtained for the control cage in which untrained L. vinosa were presented with B. amphitrite and E. modestus in the ratio of 5 to 1 are given in Table 51. The percentage of L. vinosa eating B. amphitrite is shown in figure 48.

TABLE 51. Feeding behaviour of untrained L. vinosa. The ratio of B. amphitrite to E. modestus was 5 to 1. The prey were not clumped. L. vinosa were not fed for nineteen weeks prior to the commencement of the experiment.

<u>L. vinosa</u> behaviour	2	4	Weeks		10	Total
			6	8		
Eating <u>B. amphitrite</u>	1	10	7	7	6	31
Eating <u>E. modestus</u>	1	2	1	2	0	6
Not eating	11	6	10	7	10	44

The results, plotted in figure 48, indicate that the untrained L. vinosa fed close to proportionally for all except the two week reading. The average percentage of B. amphitrite in the diet is 83.8. The 95% confidence limits are 71.7 to 95.4. These confidence limits are fairly wide and the possibility of heavier than expected predation on B. amphitrite cannot be excluded.

Proportional feeding would be an unexpected result for this experiment as both the B. amphitrite and E. modestus trained whelks fed more heavily on B. amphitrite when presented with the same prey ratio. The most likely explanation for an abnormal response in this experiment is that the nineteen week period in which the whelks were not fed was too long and affected their prey searching behaviour. In the other control experiments the whelks were starved for twelve weeks.

The feeding rate over ten weeks was close to normal (section 9.3.6), but the two week reading is abnormally low. This indicates that the whelks may not have responded to the presence of prey initially. An abnormally high number of pneumatophores which were replaced in this cage had both barnacles on them eaten. Normally the whelks are highly selective with

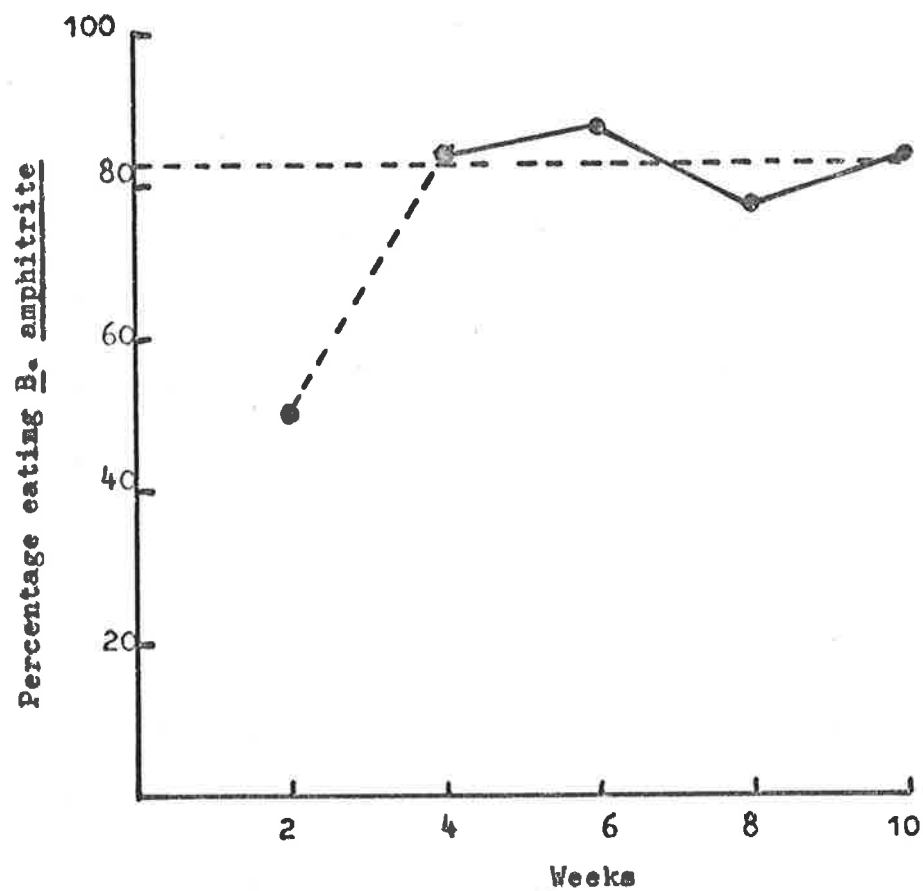


Figure 48. Percentage of L. vinosa eating B. amphitrite.

The ratio of B. amphitrite to E. modestus was 5:1. L. vinosa were not fed for 19 weeks prior to the experiment. Prey were not clumped.

regards to prey choice and often eat only one of the two available barnacles on any pneumatophore. The whelks in this experiment appeared to eat each barnacle as they encountered it without the normal rejection rate.

A comparison of the first and second observed feeds of individual L. vinosa is given in Table 52. B. amphitrite was chosen by 83.3% of the whelks in both cases. The 95% confidence limits are 58.6 to 96.4 and 51.6 to 97.9. These wide confidence limits are due to the very small sample size.

TABLE 52. First and second observed prey choice of L. vinosa in the experiment shown in Table 51. The total number of L. vinosa in each category is shown.

<u>L. vinosa</u> behaviour	<u>First observed Feed</u>	<u>Second same</u>	<u>Second different</u>
Eating <u>B. amphitrite</u>	15	7	2
Eating <u>E. modestus</u>	3	0	3

9.3.5. Statistical analysis of evidence for switching by L. vinosa in field cages.

The null case for no switching is that the expected ratio of two prey species in the diet is proportional to the ratio in the food offered. In figure 49 the expected percentage of B. amphitrite in the diet as the percentage offered varies is plotted. The curve satisfies the equation $Y = \frac{100CX}{(100-X+CX)}$ (Murdoch 1969) where X is the percentage of B. amphitrite in the food presented, Y is the predicted percentage of B. amphitrite in the diet and C is the proportionality constant which was calculated to be 1.26 (section 9.3.3).

The feeding response of L. vinosa was tested at three proportions of B. amphitrite in the food offered, 16.7%, 50% and 83.3%. Given a C value of 1.26 the expected proportions in the diet are calculated to be 20.2%, 55.8% and 86.3%. If switching occurs then the percentage of B. amphitrite in the diet should be greater than 86.3% when B. amphitrite is the more

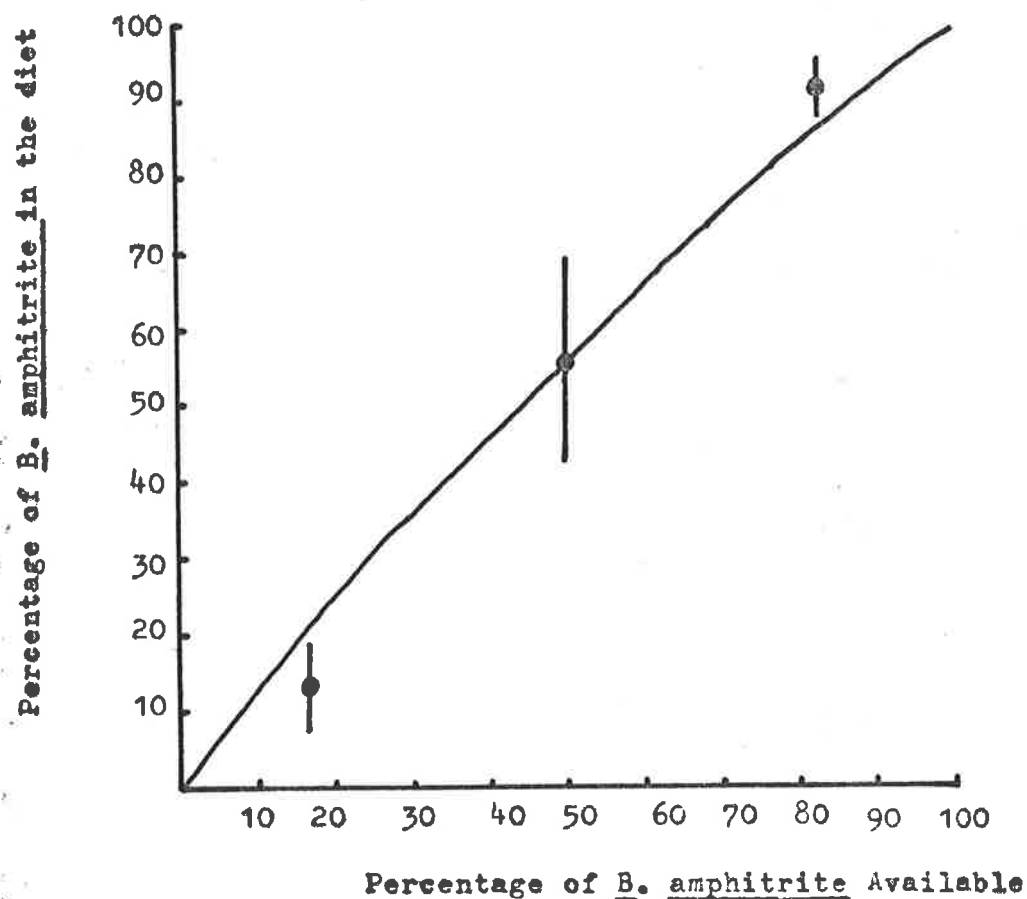


Figure 49. Expected and observed percentages of B. amphitrite in the diet of L. vinosa at different prey ratios. The mean (●) and the 95% confidence limits (vertical lines) of the results obtained from the field cage experiments are shown. The curve satisfies the equation $Y = \frac{100 CX}{(100 - X + CX)}$ where $C=1.26$ and indicates the expected feeding response if there is no switching.

abundant species and less than 20.2% when it is the less abundant species.

In the previous sections the experiments were grouped according to the prior training regimen. This approach was followed as the results of the laboratory experiments on L. vinosa and the reports in the literature on Acanthina (Murdoch 1969) indicated that marine gastropods only switch if previously trained to the more abundant species.

The mean values, except for the reverse switch to E. modestus experiments, indicate that L. vinosa switches. The 95% confidence limits for each experiment are due to the small sample size wide. This creates a problem in interpreting the results particularly as the confidence limits come close to ^{or overlap} the expected values.

The results of the field cage experiments however indicate that prior training is not necessary for switching. In Table 53 the results for all experiments, except the reverse switch to E. modestus experiments, are combined and analysed. The sample size is greatly increased in this analysis.

The results for the reverse switch to E. modestus experiments were not included as unlike the other experiments they are not consistent with switching. This is possibly due to a time lag of greater than eight weeks before a reverse switch to the less preferred prey species can be obtained. The results of the five experiments of 1 : 5 treatments are heterogeneous ($\chi^2=13.42$, 4df, $P<0.01$) when the two reverse switch experiments to E. modestus are included. If these experiments are excluded then the results for the remaining three experiments are homogeneous ($\chi^2= 0.826$, 2df).

TABLE 53. Proportions of L. vinosa feeding on B. amphitrite at different ratios of prey species offered. All results, except those for the reverse switch to E. modestus experiments, are combined.

Ratio <u>B.</u> <u>amphitrite</u> to <u>E. modestus</u> offered	Ratio <u>B.</u> <u>amphitrite</u> to <u>E. modestus</u> in diet	Expected percentage in diet	Observed percentage in diet	95% confidence intervals	$\chi^2_{1\text{-tail}}$ P 0.05
5 : 1	145 : 14	86.3	91.2	86.8-95.6	2.83 significant
1 : 1	29 : 23	55.8	55.8	42.3-69.3	-
1 : 5	19 : 123	20.2	13.4	7.8-19.0	3.70 significant

The results indicate that L. vinosa switched in the field cage experiments. The 95% confidence intervals, calculated using the formula $\hat{p} \pm 1.96 \sqrt{\frac{\hat{p}\hat{q}}{n}}$ as n is large and np, nq > 5 (Zar 1974), lie above the expected value when B. amphitrite is abundant and below the expected value when it is rare. There is a significant difference, based on 1-tail χ^2 tests, between the observed and expected number of L. vinosa eating each barnacle species at both prey species ratios.

9.3.6. Feeding rate.

The influence of training regimens on the feeding rate of L. vinosa presented with different densities of prey can be assessed from the percentage of L. vinosa eating at the time of each survey. In natural pneumatophore patches the average percentage of whelks feeding during surveys was 45.2. There were no clear seasonal fluctuations (section 4.4.2). The average feeding rate of L. vinosa in each experiment is shown in Table 54. The percentages of whelks feeding at two week intervals are plotted in figures 50 to 58.

The feeding rate of untrained L. vinosa which were presented with equal numbers of B. amphitrite and E. modestus was 46.7. This is close to average observed feeding rate in the field and indicates that the total density of prey used in the cage experiments is sufficiently high for normal feeding. The prey density was rigorously maintained over the twelve week period in this experiment. In other experiments the prey density was not rigorously maintained after four weeks and this would account for the general decline in feeding rate

towards the end of some of these experiments.

The E. modestus trained whelks, figures 53 to 55, showed a normal feeding rate particularly in the first month. This indicates that training to E. modestus does not affect the acceptability and rate of consumption of barnacles of either species.

The B. amphitrite trained whelks, however, only fed at a normal rate when presented with a mixture of prey in which B. amphitrite was more abundant. This is shown in figure 57 and the feeding rate over 10 weeks averaged 33.2.

There is no significant difference between the feeding rate of B. amphitrite trained whelks and E. modestus trained whelks when B. amphitrite was more abundant ($\chi^2=0.0346$, $df=1$, $P>0.05$).

In figures 56 and 58 the response when E. modestus was more abundant is shown. The feeding rate is markedly reduced. The percentages of whelks feeding were only 16.2 and 24.6. There is a significant difference between the feeding rate of B. amphitrite trained whelks and E. modestus trained whelks in both the unclumped ($\chi^2=12.3$, $df=1$, $P<0.01$) and the clumped design experiments ($\chi^2=3.15$, $df=1$, $P<0.05$) when B. amphitrite is the less abundant prey. The failure of B. amphitrite trained whelks to accept or detect E. modestus is the cause of this difference in feeding rates.

In the control experiments the average feeding rates were normal. When equal numbers of prey were presented the initial feeding rate after 48 hours was low. It rose higher than normal in the 2 and 4 week readings, but, then dropped back to normal. The results are plotted in figure 50. The initial low feeding rate indicates that after being not fed for twelve weeks the whelks did not immediately begin to search for prey.

A similar trend is shown in figure 51 for L. vinosa which were not fed for nineteen weeks. In this case the low feeding rate is evident after two weeks and a higher than average feeding rate is not attained until the 4 week survey. In this experiment B. amphitrite were more abundant.

The control experiment in which E. modestus was more abundant had higher than normal feeding in the 2 and 4 week readings. This is shown in figure 52.

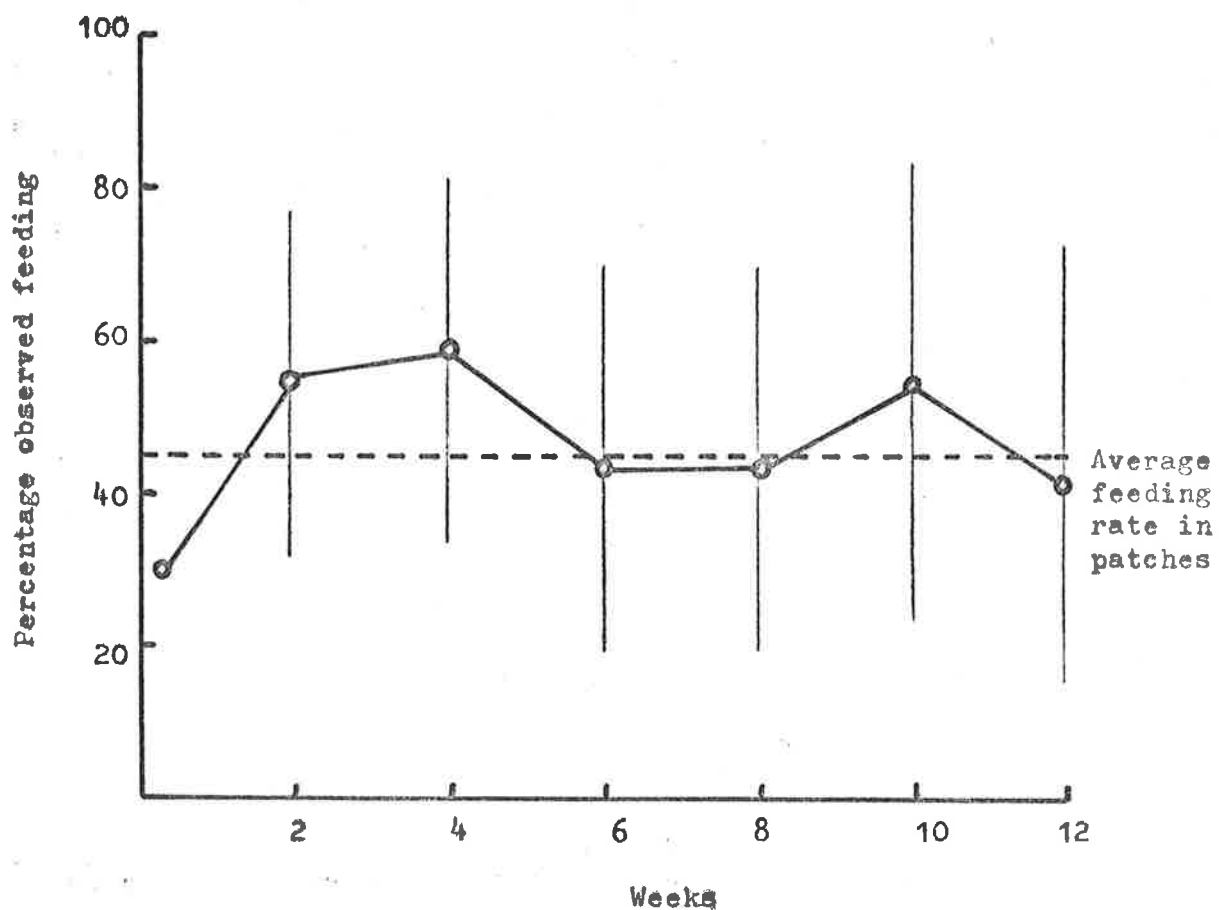


Figure 50. Percentage of *L. vinosa* observed feeding when the ratio of *B. amphitrite* to *E. modestus* was 1:1. *L. vinosa* were not fed for 12 weeks prior to the experiment. Prey were not clumped. Vertical lines indicate the 95% confidence limits.

Figure 51. Percentage of L. vinosa observed feeding when the B. amphitrite to E. modestus ratio was 5:1. L. vinosa were not fed for 19 weeks prior to the experiment. Prey were not clumped. Vertical lines indicate the 95% confidence limits.

Figure 52. Percentage of L. vinosa observed feeding when the B. amphitrite to E. modestus ratio was 1:5. L. vinosa were not fed for 11 weeks prior to the experiment. Prey were clumped. Vertical lines indicate the 95% confidence limits.

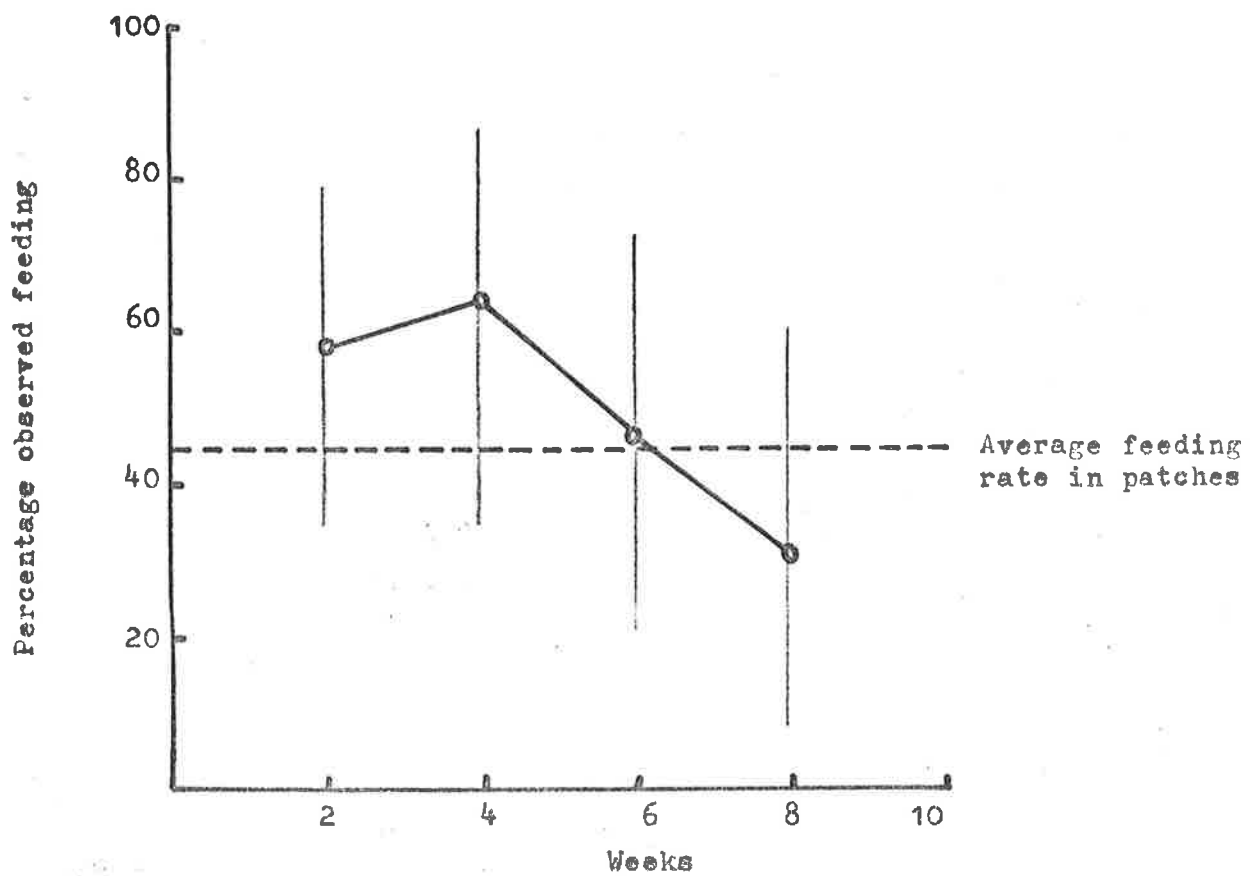
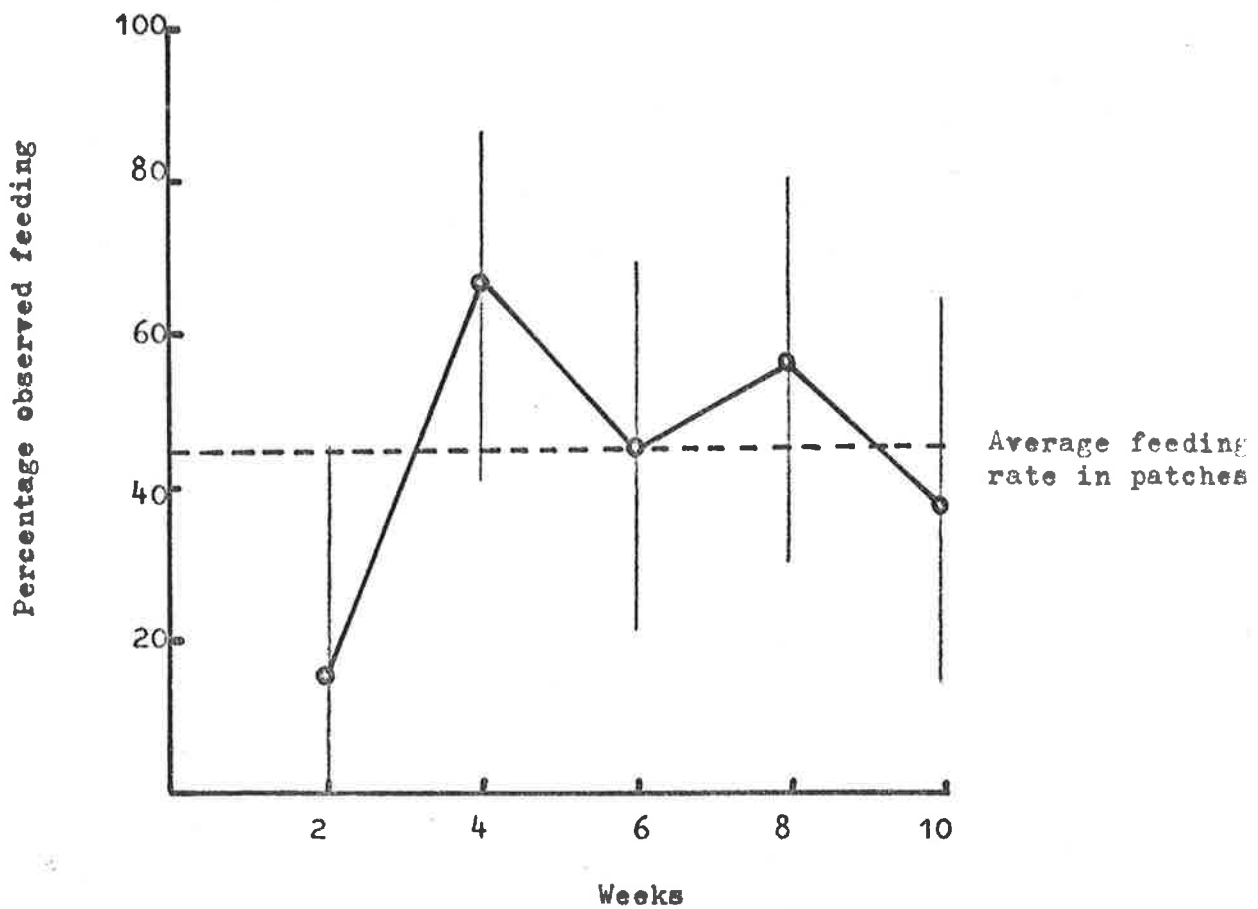


Figure 53. Percentage of L. vinosa trained to E. modestus observed feeding when the B. amphitrite to E. modestus ratio was 5:1. The mean (O) and the results of two experiments (●) are shown. Prey were not clumped. Vertical lines indicate the 95% confidence limits.

Figure 54. Percentage of L. vinosa trained to E. modestus observed feeding when the B. amphitrite to E. modestus ratio was 1:5. The mean (O) and the results of three experiments (●) are shown. Prey were not clumped. Vertical lines indicate the 95% confidence limits.

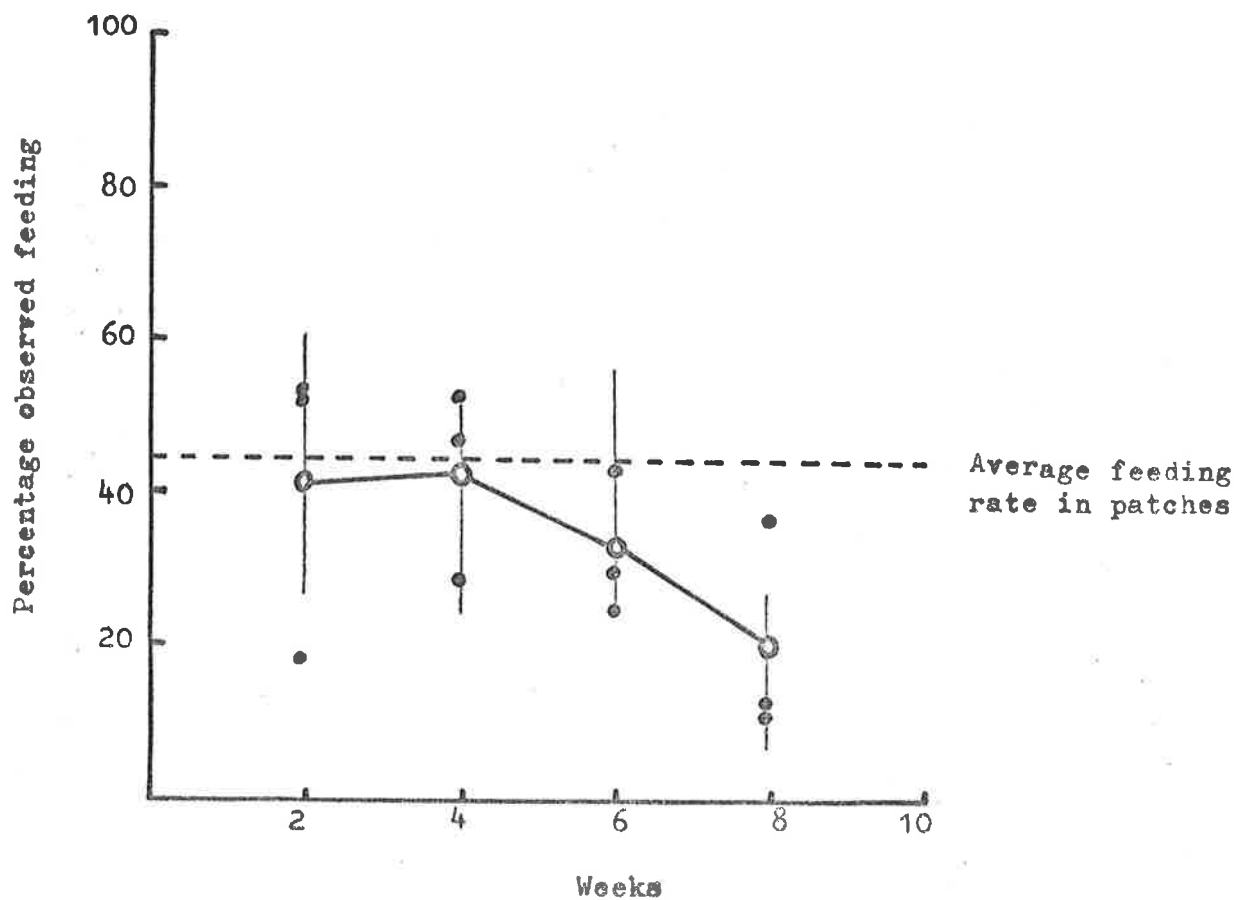
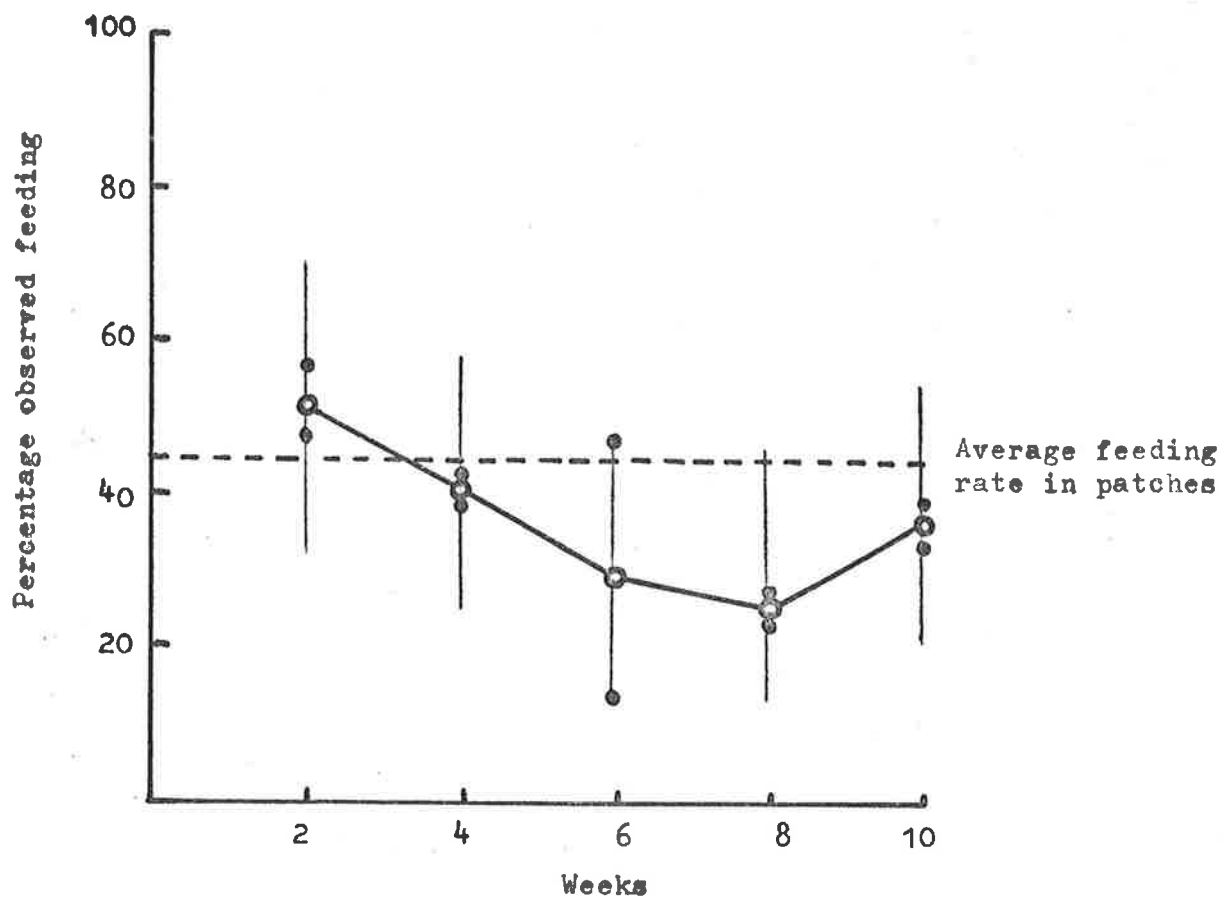


Figure 55. Percentage of L. vinosa trained to E. modestus observed feeding when the B. amphitrite to E. modestus ratio was 1:5. The mean (O) and the results of two experiments are shown (⊙). Prey were clumped.

Vertical lines indicate the 95% confidence limits.

Figure 56. Percentage of L. vinosa trained to B. amphitrite observed feeding when the B. amphitrite to E. modestus ratio was 1:5. The mean (O) and the results of two experiments (⊙) are shown. Prey were clumped.

Vertical lines indicate the 95% confidence limits.

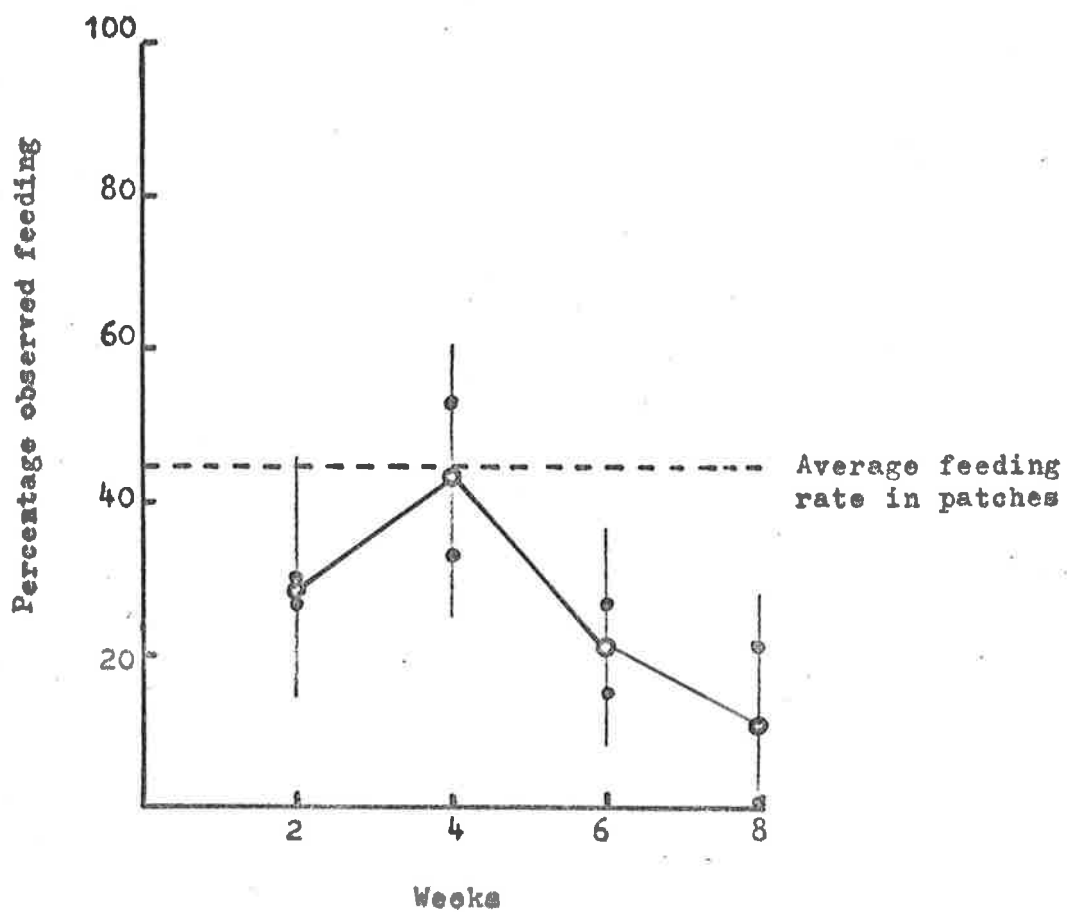
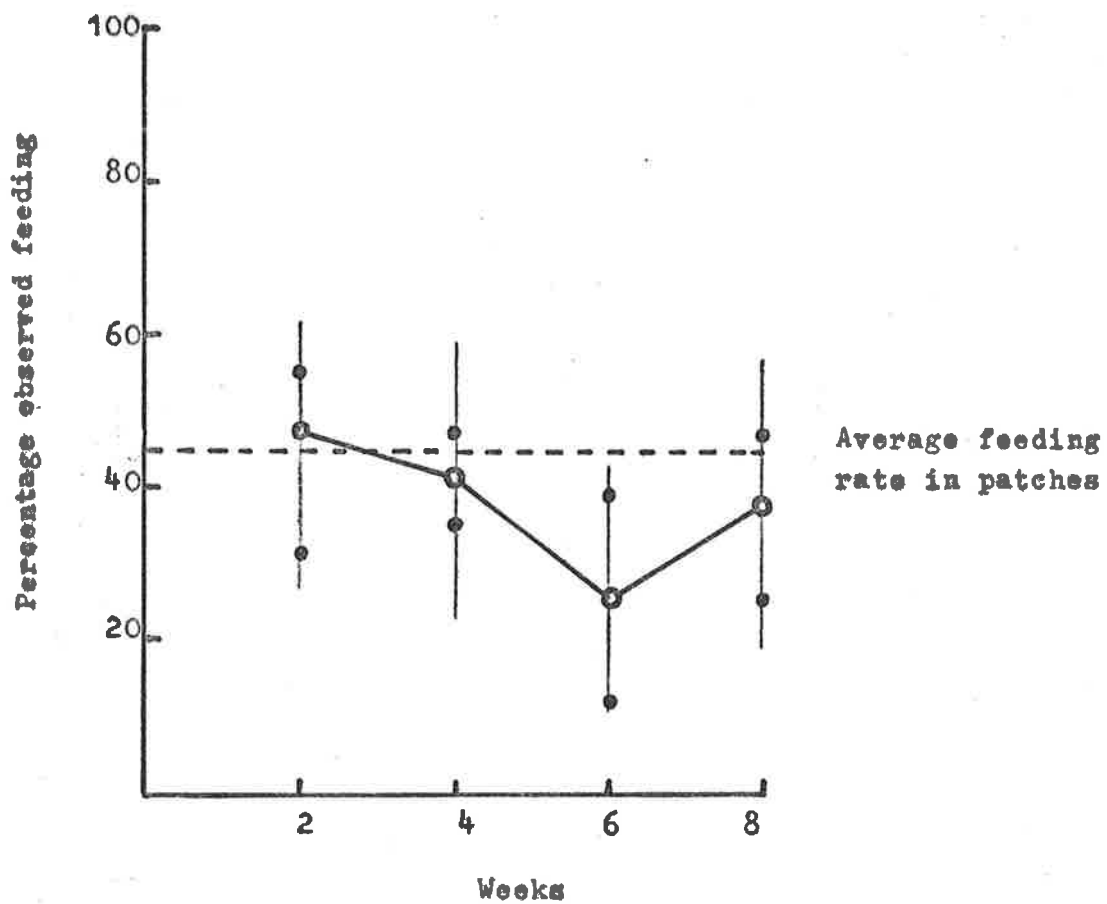
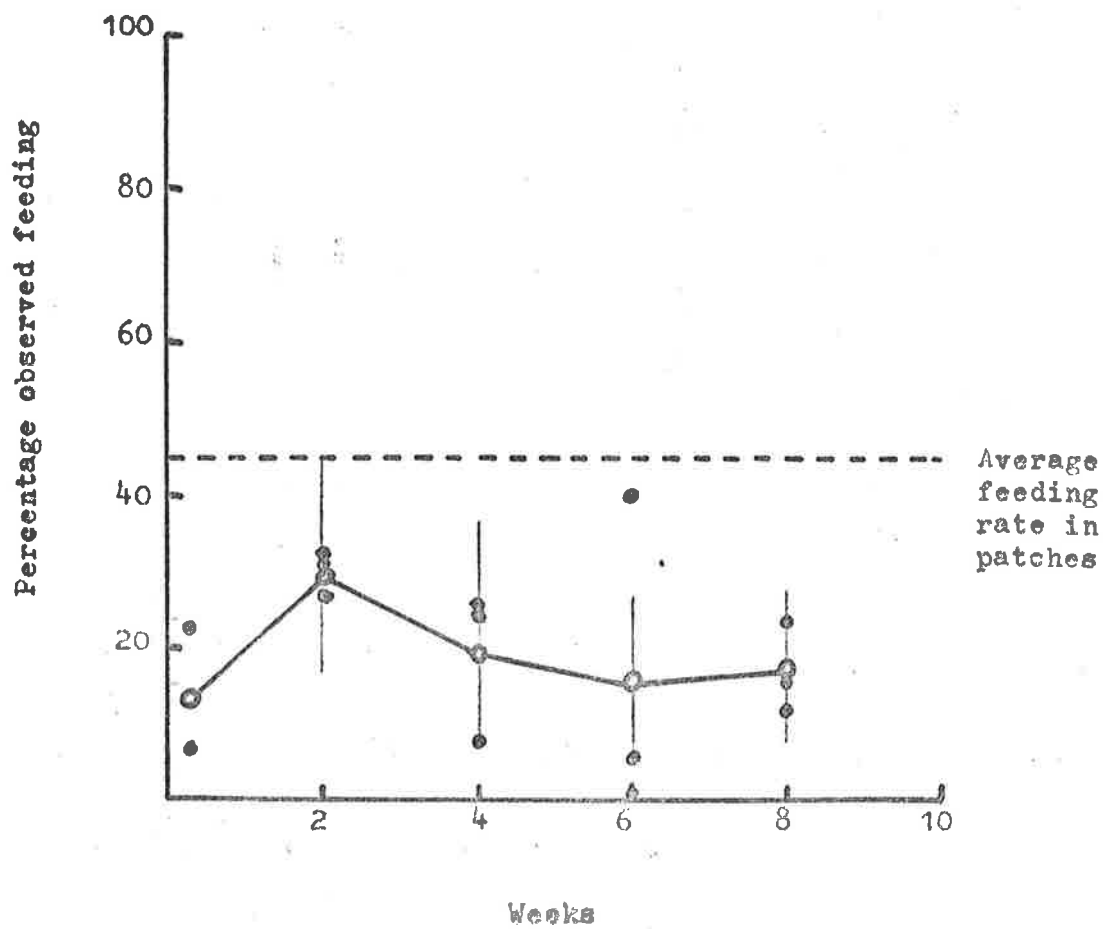
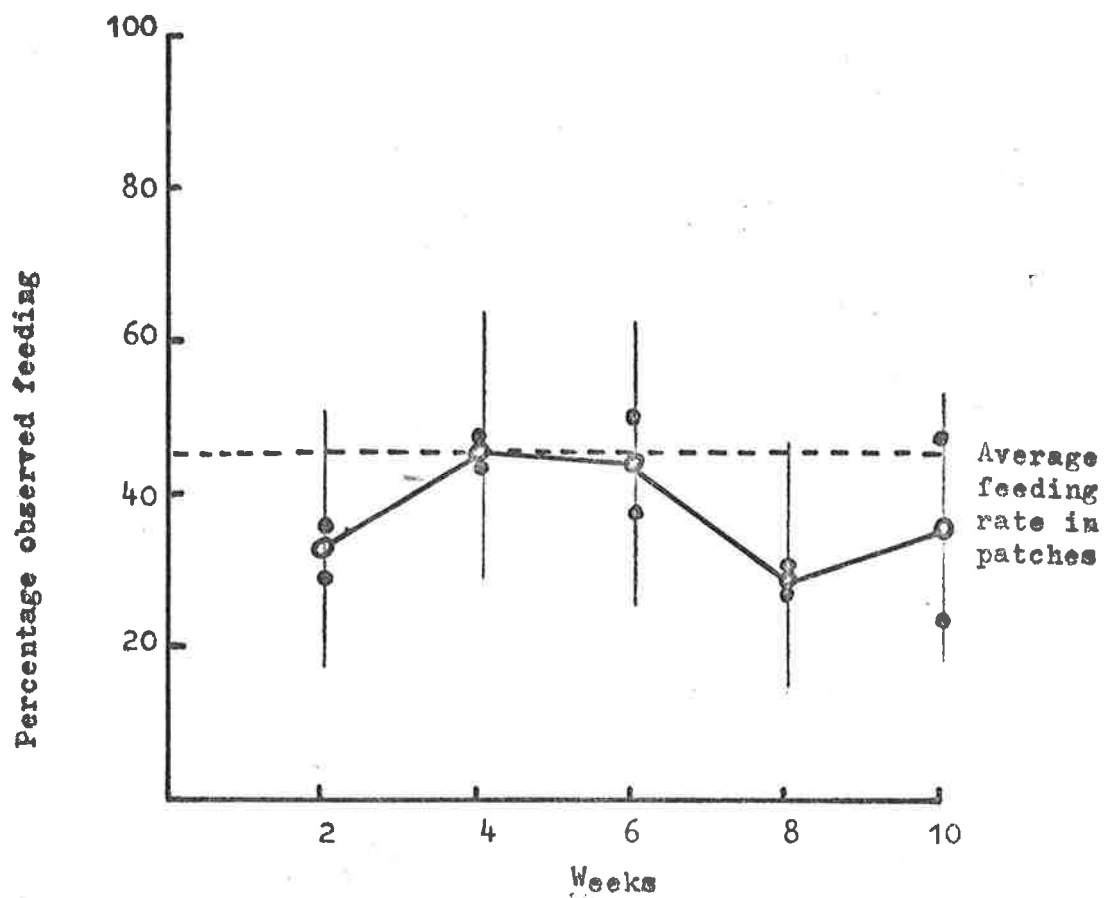


Figure 57. Percentage of L. vinosa trained to B. amphitrite observed feeding when the B. amphitrite to E. modestus ratio was 5:1. The mean (O) and the results of two experiments (●) are shown. Prey were not clumped. Vertical lines indicate the 95% confidence limits.

Figure 58. Percentage of L. vinosa trained to B. amphitrite observed feeding when the B. amphitrite to E. modestus ratio was 1:5. The mean (O) and the results of three experiments (●) are shown. Prey were not clumped. Vertical lines indicate the 95% confidence limits.



The distribution of the prey did not affect the feeding rate of L. vinosa. The E. modestus trained whelks fed at the same rate in the clumped and unclumped design experiment when E. modestus was more abundant ($\chi^2=0.258$, $df=1$, $P>0.05$). More B. amphitrite were eaten in the clumped design experiment when B. amphitrite trained whelks were presented with a prey mixture in which E. modestus was more abundant. The difference, however, is not statistically significant ($\chi^2=2.66$, $df=1$, $P>0.05$).

Seasonal effects were not apparent. The experiments were run in a series through winter, spring and summer. Experiments were paired so that whelks trained to a particular prey were tested against different prey mixtures at the same time. The lower than normal feeding rates for B. amphitrite trained whelks were obtained over a period of time when normal feeding rates were found in other experiments.

TABLE 54. Feeding rate of L. vinosa presented with different proportions of prey species following particular training regimens. The mean and 95% confidence limits are calculated from the results of individual surveys. The percentages were submitted to the arcsine transformation in both cases.

Training regimen	Ratio <u>B. amphitrite</u> to <u>E. modestus</u>	Experimental design	Mean percentage feeding	95% confidence limits
<u>E. modestus</u>	1 : 5	unclumped	32.6	15.4 - 52.4
	1 : 5	clumped	35.7	17.6 - 56.1
	5 : 1	unclumped	35.7	17.7 - 56.3
<u>B. amphitrite</u>	5 : 1	unclumped	36.9	25.4 - 49.4
	1 : 5	unclumped	16.7	6.3 - 30.9
	1 : 5	clumped	22.3	9.3 - 39.1
Control	1 : 1	unclumped	46.7	25.5 - 68.7
	5 : 1	unclumped	43.4	22.9 - 65.1
	1 : 5	clumped	49.8	27.8 - 72.1

9.3.7 Functional response and switching.

The functional response of a predator is the number of prey taken per unit time as the density of the prey population changes (Solomon 1949). It was not possible to determine the number of prey consumed per predator in the field cage experiments. Nevertheless an indication of the functional response can be gained from the percentage of predators attacking a prey species. The percentage of L. vinosa feeding on a prey species at a fixed prey density is a relative measure of predation intensity on that prey species.

Murdoch (1969) examined the functional response of a switching snail. Three prey densities were used for each species. The response when the prey species under examination was most abundant was assessed from eight snails trained to that species. The control experiment used for determining

the C value was used for the central density. Snails trained to the more abundant species were then used to assess the response to the less abundant species. Each response was therefore determined from snails with different feeding histories prior to the commencement of the experiment. Only the switching experiments were used. The overall response was sigmoidal.

In Table 55 the percentages of L. vinosa observed attacking a prey species at the three different densities which were available in field cage experiments are listed. All experiments are included and the means and standard errors at each prey density are shown. The results for the three densities of B. amphitrite show very little variation due to prior training regimen. Greater variation is obtained in the results for the three densities of E. modestus. This is due to the three experiments which did not, at least initially, produce results consistent with switching. If these experiments were ignored the results for the two species would be very similar.

The means and standard errors for each density of the two prey species are plotted in figures 59 and 60. The response ~~could~~ be sigmoidal. A sharp rise occurs for both species between the densities of 1.87 and 5.56 prey per metre of pneumatophore. Unlike Murdoch's (1969) results for Acanthina the response is not "forced" by the prior training regimen.

The similar responses to changes in the densities of the two prey species are however not produced by the same mechanism. The low rate of predation on E. modestus when its density is 1.83/metre of pneumatophore is due to a large number of L. vinosa feeding on the more abundant B. amphitrite. The low rate of predation on B. amphitrite when its density is 1.83/metre of pneumatophore is due to a large number of L. vinosa not feeding. Switching therefore only produces the sigmoidal functional response for the less preferred prey.

TABLE 55. Percentage of L. vinosa attacking barnacles at different prey densities.

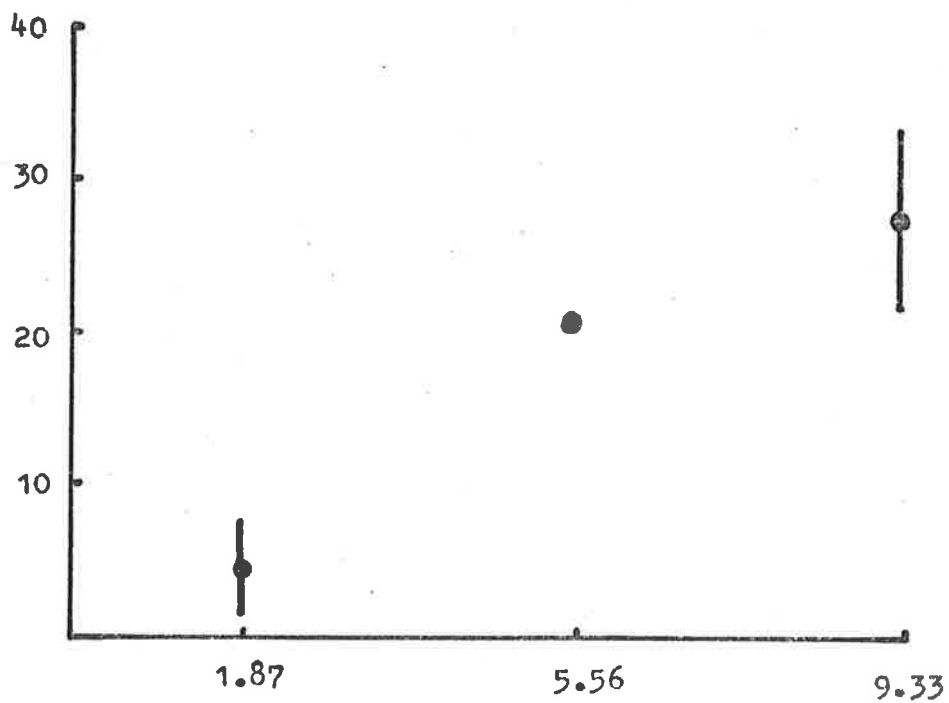
A. <u>E. modestus</u>			
Density (No./m. of pneumatophore)	Training Regimen	Percentage attacking <u>E. modestus</u>	Mean $\pm$ S.E.
1.87	<u>E. modestus</u>	2.5	
	<u>B. amphitrite</u>	2.4	
	Unfed	8.6*	4.5 $\pm$ 2.9
5.56	Unfed	20.5	20.5
9.33	<u>E. modestus</u> (unclumped)	29.3	
	(clumped)	31.1	
	<u>B. amphitrite</u> (unclumped)	11.2*	
	<u>B. amphitrite</u> (clumped)	19.8*	
	Unfed	45.9	27.5 $\pm$ 5.8
B. <u>B. amphitrite</u>			
1.87	<u>B. amphitrite</u> (unclumped)	6.9	
	<u>B. amphitrite</u> (clumped)	6.9	
	Unfed	4.9	
	<u>E. modestus</u> (unclumped)	4.3	
	<u>E. modestus</u> (clumped)	6.8	6.0 $\pm$ 0.6
5.56	Unfed	25.8	25.8
9.33	<u>B. amphitrite</u>	34.3	
	<u>E. modestus</u>	35.8	
	Unfed	37.0	35.7 $\pm$ 0.8

*Majority of readings not consistent with switching.

Figure 59. Percentage of L. vinosa attacking E. modestus at different densities of E. modestus in the prey offered.

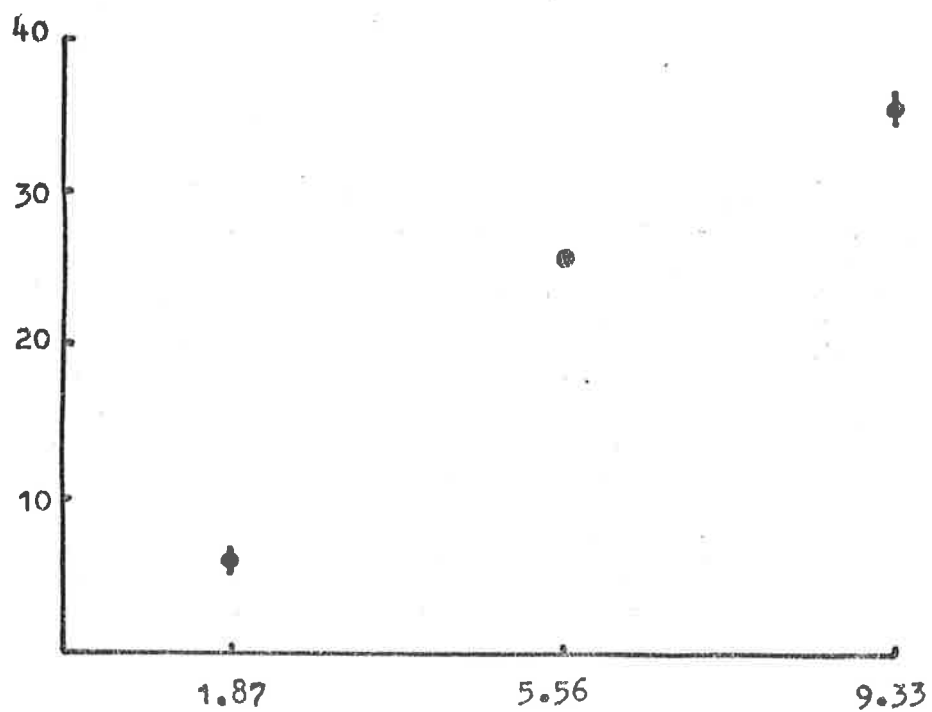
Figure 60. Percentage of L. vinosa attacking B. amphitrite at different densities of B. amphitrite in the prey offered.

Percentage L. vinosa attacking E. modestus



Number E. modestus per metre pneumatophore

Percentage L. vinosa attacking B. amphitrite



Number B. amphitrite per metre of pneumatophore

9.3.8.

Influence of absolute density on predation.

The results obtained from field surveys, reported in section 7.4, indicate that absolute density as well as relative density influences predation on the barnacle species. In the previous field cage experiments the absolute barnacle density was fixed and only the relative density of the prey species varied. In the following experiment the relative density of the prey species is fixed and the absolute density varies. The effect of this variation in absolute density on the number of prey of each species which were consumed by L. vinosa with different training histories is assessed.

A different experimental procedure was followed in this experiment to determine both the number of each species of barnacles consumed and the relative proportion each species forms in the diet. To determine accurately the number of barnacles eaten in a given period of time both the duration of the experiment and the size of the artificial patches must be reduced.

Four cages, each enclosing an area of 0.25sq. metres, were used. The pneumatophores were 18cm long, 128 per cage, and the prey on them were not clumped. The prey ratio in each cage was 1 B. amphitrite to every 5 E. modestus. In two cages the absolute density of barnacles was 11.2/metre of pneumatophore. In the other two cages it was 56/metre pneumatophore. The lower density is the same as that which was used in the switching experiments.

Ten L. vinosa were placed in each cage. The whelks had been trained to either E. modestus or B. amphitrite by being fed pure diets for twelve weeks. One group of whelks of each training history were used at each density. The whelks were allowed to feed for fourteen days. At the conclusion of the experiment all pneumatophores were removed and examined later in the laboratory. The numbers of dead barnacles were recorded. It was assumed that predation was responsible for all mortality.

No mortality occurred in a control cage in which 100 prey of each

species were left without any predators being present. No L. vinosa died or escaped from any cage.

The number of each prey species consumed in each of the four cages is shown in figure 61. The maximum feeding rate was 1.65 barnacles/L. vinosa/week which was obtained from the E. modestus trained L. vinosa in a high density cage. There is no significant difference between the total number of barnacles eaten by the B. amphitrite and E. modestus trained L. vinosa in high and low prey density cages ($\chi^2 = 0.028$, $n = 86$, $df=1$, $P>0.05$).

The number of B. amphitrite compared to E. modestus consumed in the two high density cages is however significantly greater than the number consumed in the two low density cages ($\chi^2 = 13.8$, $n = 86$, $df = 1$, $P<0.01$). In the low density cage L. vinosa trained to E. modestus fed close to proportionally. A five fold increase in the barnacle density led to more B. amphitrite being consumed and the proportion this species formed in the diet was 52%. The difference is statistically significant ($\chi^2 = 5.36$, $n = 56$, $df = 1$, $P<0.05$).

In the low density cage L. vinosa trained to B. amphitrite ate no B. amphitrite although in the high density cage it formed 58% of the diet. The difference is statistically significant (Fisher's exact probability test, $P = 0.0014$). Feeding in the low density cage by L. vinosa trained to B. amphitrite is low compared to other cages and this may be due to less vigorous searching for prey. This could occur if searching behaviour was stimulated by the density of acceptable prey.

The results are consistent with the hypothesis, proposed in section 7.6, that relative and absolute prey density are interacting factors. A further rise in absolute density should result in the eventual elimination of nearly all of the less preferred prey from the diet despite its greater relative abundance.

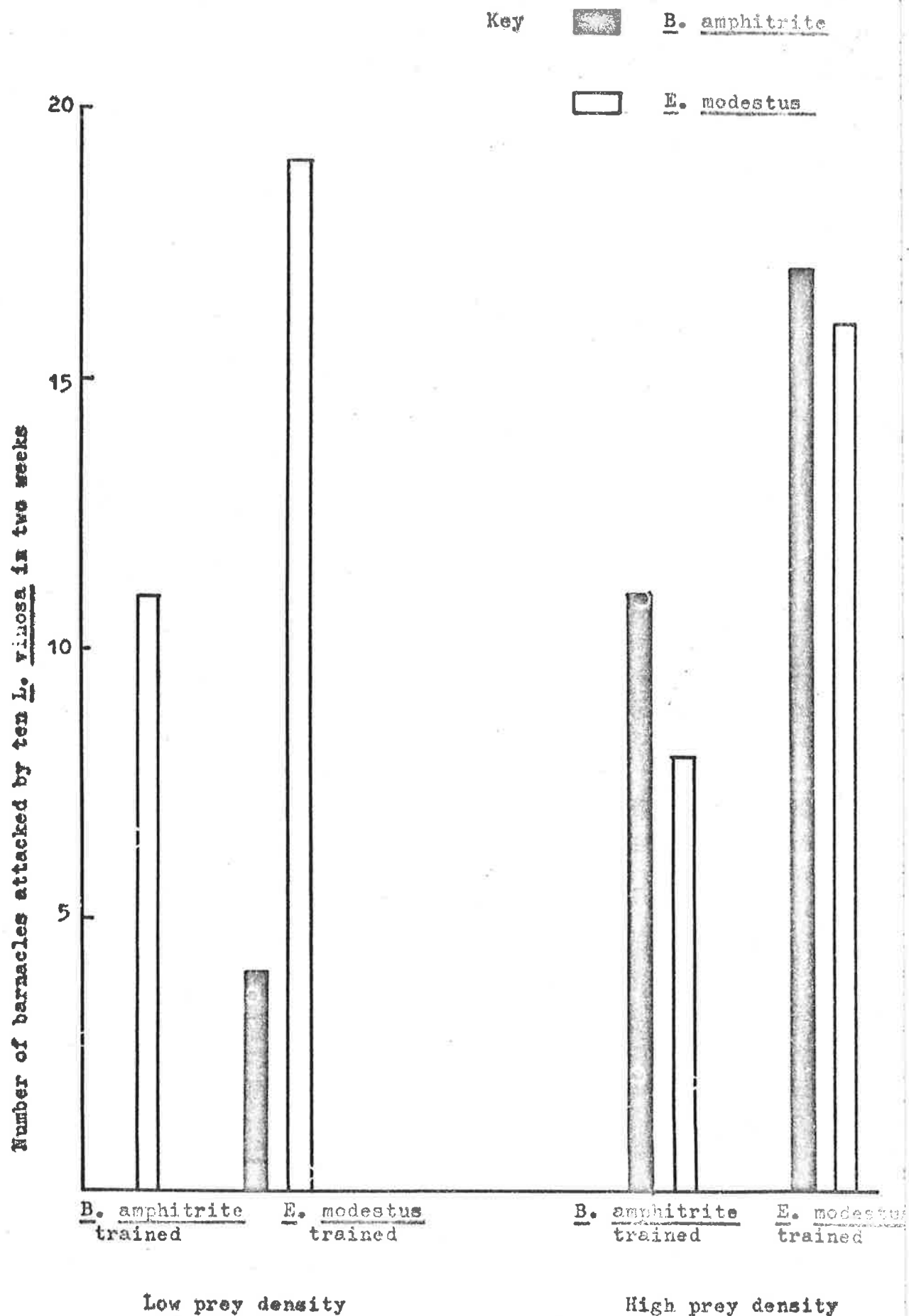


Figure 61. Number of barnacles attacked in two weeks by groups of ten L. vinosa trained to each prey species at two different prey densities. The ratio of B. amphitrite to E. modestus was always 1:5.

9.4 Discussion

The results obtained from the field cage experiments indicate that switching can take place in the field if the abundance of the preferred prey species is not too high. The switch is maintained over a period of at least eight weeks and there is no trend to proportional feeding.

Murdoch's (1969) model of a switching gastropod requires feeding on a pure diet to produce the switching. In the field, unlike the laboratory, L. vinosa switches to the more abundant species irrespective of the previous training regimen if sufficient time is allowed. Prior training is therefore not required to force the switch.

The feeding response of L. vinosa is highly asymmetrical with respect to the two prey species. The switch to the preferred prey species is stronger than to the less preferred prey species. Furthermore L. vinosa immediately reverse switches to the preferred prey species. The alternative reverse switch to the less preferred prey species, however, requires either a clumped prey distribution or if the prey are evenly distributed a period of longer than eight weeks.

There is also a marked asymmetry in the feeding rate. L. vinosa which have been trained to E. modestus always feed at the normal feeding rate irrespective of the relative abundance of the two prey species. Those which were trained to B. amphitrite, however, show a marked reduction in their feeding rate when B. amphitrite is less abundant.

Asymmetry in the switching and feeding rate response may be a general feature of gastropod predators. Results obtained in laboratory experiments with Acanthina (Murdoch 1969) show a similar reverse switch asymmetry to that shown by L. vinosa. Both gastropods failed to reverse switch to the less preferred prey species. Murdoch (1969) claimed that Acanthina reverse switched to the preferred prey species. An examination of the results, however, reveal a trend to proportional feeding.

Proportional feeding was obtained in the corresponding laboratory experiments for L. vinosa.

Luckens (1970) has reported an asymmetrical feeding rate response for Ocenebra following conditioning to Mytilus edulis and Chthamalus challengerii. Ocenebra which were conditioned to the preferred prey, Chthamalus challengerii, will not accept Mytilus edulis for long periods. However whelks which were conditioned to the less preferred prey, Mytilus edulis, will immediately feed on either prey species.

L. vinosa has a weak preference for B. amphitrite at equality. The same value for C, 1.26, was obtained in the field as in the laboratory. The preference appears to be consistent between individual predators. There is no evidence that any of the predators specialised on either prey species. Successive observations of marked individuals indicated close to random prey selection. In the laboratory experiments the variation between replicates was 47% to 67% B. amphitrite in the diets. This indicates a central tendency and a lack of specialisation on one prey species.

Variability in preference at equality was found for Acanthina by Murdoch (1969). The prey used in this experiment were barnacles and mussels and the predator required a different technique to attack each prey type. This is probably the reason for the variability between individuals. In the same paper Murdoch reports that Thais when offered two mussel species had consistent preferences at equality. L. vinosa was offered two barnacle species and like Thais did not have to change.

its attack technique when feeding on both species. Thais is reported to not switch, but, the C value was 10 indicating a very strong preference for one species.

Murdoch and Oaten (1975) argue that there should be a relationship between weak variable preferences at equality and switching. Their rationale is that a weak preference and similar diets at equality indicate an indiscriminate choice between prey and suggests that conditioning or

training cannot be obtained by feeding upon one of the prey species. Experimental evidence to support this hypothesis comes from studies on ladybirds (Murdoch and Marks 1973), the mite Zetzellia mali (Santos 1976) and bluegill (Reed 1969 reported in Murdoch and Oaten 1975).

Predators reported to switch have usually shown variable preferences at equality. Murdoch and Oaten (1975) have examined data on pigeons (Murton 1971) and Stentor (Rapport unpublished data) and claimed that these studies support their generalisation. Guppies (Murdoch et al., 1975) also have weak but variable preferences at equality. Lawton et al. (1974) have reported that Notonecta changed from variable to consistent preferences during the course of their experiments.

Murdoch et al. (1975) have, however, conceded that switching could occur for a predator showing consistent weak preferences at equality provided that attack success rather than preference varied. This concession is based on the mechanism proposed by Lawton et al. (1974) to explain switching in Notonecta. The results from this study of switching in L. vinosa indicate that switching can be associated with weak consistent preferences. The generalisation is based on too few studies and should be discarded rather than modified. Given the ability to become trained to either prey species there is no apparent reason why variable or consistent preference at equality should be a factor in preventing a switching response.

Murdoch (1969) considered variable rejection rates as the mechanism producing switching in Acanthina. This hypothesis is used as the basis for later mathematical models (Oaten and Murdoch 1975).

Variable rejection rates may explain switching in laboratory experiments on marine gastropods, but I doubt if it is the sole mechanism which operates in the field. Rejection of prey after thorough examination is certainly one important factor for L. vinosa (section 4.2).

Detection of prey at a distance should also be important. Pratt (1974) has suggested that feeding by Urosalpinx is governed by sequential stimuli which elicit appropriate behaviour. Search and attack are different behaviours and he argues that two distinct stimuli are involved.

Carnivorous gastropods detect their prey by chemoreception (Kohn 1961). Wood (1968) demonstrated that whelks respond to effluents from living prey and that individuals develop a preference for a prey species by "ingestive conditioning." Urosalpinx does not respond to effluent of some potential prey species unless previously fed that species (Wood 1968, Pratt 1974). Nevertheless the preferred prey species remains attractive (Wood 1968, Pratt 1974) and will be fed upon even if the whelks are taken from localities where it is absent (Fischer-Piette 1935, Moore 1936 and Hancock 1960).

Switching implies a numerical result rather than a mechanism (Murdoch and Oaten 1975). No attempt was made in this study to investigate directly the mechanism involved in the switching response. It is possible that L. vinosa forms a chemical "search image" for a prey species after being fed consecutive meals of that prey species. Olfactory cues have been reported to be responsible for apostatic selection by mice (Soane and Clarke 1973).

This "search image" would be different to Tinbergen's (1960) search image in a number of respects. Exposure to the stimulus, that is effluent from the prey, would not lead to its formation. Wood (1968) has demonstrated that the prey must be eaten to influence effluent detection by Urosalpinx.

In addition it would operate primarily by altering the sensory detection threshold for the less preferred prey species. Stimuli from E. modestus may be weaker than from B. amphitrite. The threshold would be lowered if L. vinosa were trained to E. modestus or starved. Feeding on B. amphitrite would raise the threshold. If the threshold for the preferred prey species could be lowered but not raised above its normal level then

the asymmetry in the results, as well as studies reported in the literature, could be explained.

Sensory detection thresholds are more likely to be exceeded when prey are clumped (Taylor 1977). Concentration of prey effluent can make an unattractive prey species attractive to Urosalpinx (Pratt 1974). Clumping of prey leads to predators which hunt by search images being more successful (Tinbergen et al. 1967, Croze 1970). Effluent strength from pneumatophores with prey in the clumped design experiments should be either 250% or 500% stronger than from pneumatophores in the unclumped design experiments. This could be sufficient to affect the whelks' ability to detect the less preferred species.

The results of the experiments on reverse switching to the less preferred prey species give some support to this hypothesis. The number of L. vinosa observed attacking E. modestus almost doubles from 11.2% in the unclumped experiments to 19.8% in the clumped experiments. The number of L. vinosa attacking B. amphitrite remains nearly the same with 6.9% observed in the unclumped and 6.1% in the clumped. Furthermore clumping had no effect in any other experiments.

Random searching followed by variable rejection rates would be inadequate to explain these results. In the unclumped design experiments every pneumatophore had prey present and a predator which searched randomly should not have a low encounter rate compared to the clumped design. The more abundant species would also be present on each pneumatophore.

There are no data available in the literature on the functional response of invertebrate predation in the field (Murdoch and Oaten 1975). Murdoch (1973) states that switching under many circumstances produces a type 3 response for the preferred species. The response to the less preferred prey is predicted to be frequently not stabilising. It is only stabilising when the preferred species is decreasing at the same time as the less preferred prey is increasing. A type 2 response is predicted for the preferred species when it is increasing faster than the non-preferred species. These predictions are not supported by the data

obtained in the field experiments for L. vinosa.

L. vinosa appears to have a type 3 functional response to both prey species in the field (section 9.3.7). The densities used in the experiments are typical of those found in inland patches and it can be concluded that L. vinosa has a potentially stabilising influence on both its prey species.

A settlement of the preferred prey species could increase both its relative and absolute abundance. If there was not a corresponding settlement rate for the less preferred species its density would increase faster. In this situation I would expect the increase in relative and absolute abundance to have a cumulative effect on the rate of predation on the preferred species. The sigmoidal curve should become more pronounced. A plateau would be reached, if the settlement was heavy, as there is a limit to the number of barnacles which can be consumed per unit time.

Total prey density as well as the relative frequency of the two barnacle species influences the prey selection of L. vinosa. Three different responses to the abundance of prey species are possible.

At very low total densities feeding should be proportional to relative abundance of each prey species. Control animals which were starved for nineteen weeks fed proportionally. This result was probably due to animals which were in a poor nutritional state, accepting each prey as encountered. Prey scarcity in the field should also produce this effect. The predator could not afford to ignore any food item.

At moderate densities switching occurs and this response probably increases feeding efficiency. The predator is probably more efficient at locating prey if it concentrates on the stimuli from only one species. If the predator is to maintain a significant rejection rate following prey evaluation it would be advantageous to concentrate on the more abundant species. Concentration on one species may also be more efficient physiologically (Murdoch and Oaten 1975).

At high prey densities L. vinosa concentrates its attacks on the preferred prey species and ignores the less preferred species. There is no advantage in doing otherwise unless variety is required in the diet. It was argued in section 7.6 that this is compatible with optimal foraging.

Changes in total prey density have been found to influence prey selection in studies on apostacy. Cook and Miller (1976) report that frequency dependent selection acts to maintain a visual polymorphism only at intermediate densities. Greenwood (1969) suggests that frequency dependent selection protecting the rare forms will be more effective at intermediate levels. This is because the fraction of a food source taken by a predator is likely to be small when density is either low or high.

Allen (1972) reported an example of frequency dependent selection by wild birds at low densities which was not maintained at high densities. At high densities the rare form was taken. This is however probably due to the experimental design in which so many of the more common form were present that they formed a visual background for the rare form.

It must be concluded that the design of switching experiments should include provision for an examination of the effect of varying the absolute abundance of the preferred prey species while maintaining a fixed relative abundance compared to the less preferred prey species.

CHAPTER 10

General discussion on the stability of the interaction between *L. vinosa* and barnacles.

In the laboratory predator-prey interactions are unstable and the prey become extinct (Gause 1934, Huffaker 1958). There has been much speculation on mechanisms which could be responsible for stability in a predator-prey interaction in the field. In conclusion I wish to indicate those mechanisms which appear capable of contributing to stability in the interaction between *L. vinosa* and barnacles.

Evidence has been produced which indicates that refuges (section 3.6) and the switching behaviour of the predator (section 9.3.7.) contribute to the stability of the interaction. Spatial heterogeneity should contribute to the stability of a predator-prey interaction (Royama 1971, Hassell and Rogers 1972, May 1973). It would be difficult to assess the relative importance of each of these mechanisms as they are all operating together.

In section 3.8 it was suggested that the interaction between *B. amphitrite* and *E. modestus* could be stable without a predator being present. The superior competitive powers of *B. amphitrite* are offset by the shorter generation time and the superior dispersal and reproductive capacity of *E. modestus*.

A non-switching predator could exert some stabilising influence in this situation (May 1977), if predation had greater effect on the dominant species (Paine 1966, van Valen 1973). Equivalent predation, however, cannot make any difference to the competitive coexistence among prey species (van Valen 1974, May 1975). Switching could however allow the predator to coexist successfully with the two prey species (Comins and Hassell 1976) and increase the extent of niche overlap between the prey species (Roughgarden and Feldman 1976).

Asymmetry in the switching response could be a further stabilising factor. *L. vinosa* has a time lag in switching from *B. amphitrite* to *E. modestus*

which is in the order of six weeks or longer. Given the rapid growth and continuous breeding season of E. modestus there is a possibility that this would be long enough for another generation of larvae to be released into the plankton. Provided that the competitively superior B. amphitrite remains abundant then a heavy E. modestus settlement is not immediately subjected to heavy predation. A heavy B. amphitrite settlement is however immediately subjected to heavy predation. The weaker species in competition is therefore favoured.

There is little information in the results on the importance of the predators' rate and pattern of dispersal. In chapter 6 it was shown that some whelks are highly mobile. This would increase the feeding efficiency of the predator population in a patchy environment.

Hassell and May (1973 and 1974) consider differential aggregation in areas of high prey density to be important in stabilising predator-prey interactions. L. vinosa does not aggregate in sufficiently high numbers in any patch for this to be a major factor.

No information was collected on the developmental response (Murdoch 1971) and the numerical response (Solomon 1949) of the predator. These factors could potentially contribute to stability.

Some marine invertebrates, Balanus cariosus (Connell 1972) and Mytilus californianus (Paine 1976), have been reported to grow too large to be attacked by their predators. They form an invulnerable class of prey once a certain body size is attained. L. vinosa is capable of attacking barnacles of either species irrespective of size. There is no refuge in size in this predator-prey interaction.

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