Factors determining the distribution and abundance of the abalone *Haliotis cyclobates* Péron, 1816, at Edithburgh, South Australia.

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CONTENTS

ABSTRACT

At Edithburgh, South Australia, the abalone *Haliotis cyclobates* occurs on patches of hard substrata in seagrass meadows, although high densities of abalone occasionally occur in open areas. I investigated the role of predation, food abundance and accessibility, and the behaviour during early life history (ELH) of *H. cyclobates*, in determining its local distribution and abundance. Access to an abundant supply of food, and recruitment patterns established during the ELH, best explain the observed patterns. Larvae apparently settle predominantly on seagrass blades, establishing high densities of recruits in seagrass areas. Older juveniles and adults were found to move regularly between substrata if food was absent, but not if an abundant food supply was present. Seagrass meadows were the most likely source of abundant food, hence the predominant occurrence of abalone in them. An open area that naturally supported a high density of abalone was found to be frequently covered by large mats of drift-weed, which would provide the necessary source of abundant food. Predation was found to have no effect on the distribution and abundance of *H. cyclobates*. Further work is suggested in several areas, particularly on the role of drift algae in determining local distributions, and the settlement cues for this species.

STATEMENT OF AUTHENTICITY

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other teritiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

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CHAPTER 1 INTRODUCTION

1.0 Introduction

Distribution and abundance patterns of organisms vary across time and space. Mapping these variations is essential if appropriate hypotheses about the controlling processes are to be made (Andrew & Mapstone, 1987). Factors that cause variations are temporal and spatial changes in physical conditions, abundance of predators, pathogens and competitors, availability of food and shelter, and the dispersal of juveniles. Frequently, different processes produce similar patterns so careful observation is required to avoid erroneous conclusions about the biology and ecology of an organism.

In this study I have investigated the local distribution of the abalone *Haliotis cyclobates* Péron, 1816. Unlike most abalone species, it inhabits small isolated rocks and is frequently associated with seagrass meadows (Shepherd, 1973). It has been suggested that its distribution is determined by predators (Shepherd, 1973), although other factors have not been studied.

1.1 Distribution & Abundance

Abalone commonly occupy rocky reefs, ranging from the intertidal to depths of 30-40m (Poore, 1972; Shepherd, 1973; Mottet, 1978; Hines & Pearse, 1982; Clavier & Richard, 1986; Peck & Culley, 1990; Wells & Keesing, 1990). Across a reef-slope several species can co-exist, each occupying a separate niche (Shepherd, 1973). Past competition may have initiated this segregation, but it fails to explain existing patterns because common resources are usually abundant (Shepherd, 1973). A variety of other processes, including predation, food availability and behaviour during early life-history stages have been cited

as factors controlling the distribution of abalone (Poore, 1972; Hines & Pearse, 1982; Shepherd & Turner, 1985; Tong *et al.*, 1987; McShane *et al.*, 1988; Wells & Keesing, 1990; McShane, 1991; Andrew & Underwood, 1992; Shepherd *et al.*, 1992). The importance of each process may vary for each species, depending on habitat, size, shell morphology and diet. Frequently two or more processes or spatio-temporal changes may be involved (Sale, 1990), creating a unique set of parameters that determine the distribution of each species.

1.2 Predation & Food Availability

Predation and food availability are often cited as important factors influencing the local distribution and abundance of marine organisms (Shepherd, 1973; Coen *et al.*, 1981; Leber, 1985; Moran, 1986; Main, 1987; Holbrook & Schmitt, 1988; Arrontes, 1990; Lubbers *et al.*, 1990; Olla & Davis, 1990; Duffy & Hay, 1991; Irlandi & Peterson, 1991; Eggleston & Lipcius, 1992). Both can affect the foraging behaviour of animals (Hines & Pearse, 1982; Sih, 1987; Macchiusi & Baker, 1992), and may result in a species occupying a particular habitat in preference to adjacent habitats (Bell & Westoby, 1986).

Foraging increases the risk of predation for both active and passive foragers (Peterson & Quammen, 1982; Navarrete & Castilla, 1990; Irlandi & Peterson, 1991; Pecon-Slattery *et al.*, 1991; Johnsson, 1993; Utne *et al.*, 1993). Encounters with predators can be minimised by various strategies (review by Sih, 1987); these include foraging in or near refuges (Shepherd, 1973; Duffy & Hay, 1991; Macchiusi & Baker, 1992; Legault & Himmelman, 1993). Refuges may be rich or poor in food so restriction to a particular refuge may have pronounced effects on demography (Sih, 1987). Complex habitats (e.g. vegetated areas)

provide good refuges to numerous species (Peterson, 1982; Werner *et al.*, 1983; Summerson & Peterson, 1984; Main, 1987; Gotceitas & Colgan, 1989; Duffy & Hay, 1991; Pecon-Slattery *et al.*, 1991) and are frequently food-rich (Shepherd, 1973; Irlandi & Peterson, 1991). Foraging times are reduced when food is abundant (Macchiusi & Baker, 1992), so occupying food-rich refuges would further minimise exposure to potential predators. The occupation of food-rich habitats is, however, adaptive in itself, and so should be displayed even by species not threatened by predation. Foraging uses energy and if this can be minimised more will be available for growth and reproduction (Pyke, 1984).

Therefore, in investigating the local distribution and abundance of a species, hypotheses concerning food availability and predation must be considered as possible explanations, and these are not mutually exclusive.

1.3 Recruitment Variability

Variations in juvenile recruitment patterns over time and space can have important consequences for adult distributions and abundances (Roughgarden *et al.*, 1984, 1985, 1988; Underwood & Denley, 1984; Connell, 1985; Gaines *et al.*, 1985; Milicich & Doherty, 1994). Variable recruitment can promote the stable co-existence of species, alter patterns of gene flow, or affect the management of commercially important species (Chesson, 1985; Butler & Chesson, 1990; Fogarty *et al.*, 1991; Gaines & Bertness, 1992).

Recruitment variation is common amongst abalone populations (McShane & Smith, 1991; Shepherd & Brown, 1992). Patterns of recruitment are determined by the cumulative effects of processes operating throughout the early life history stages. Identifying these processes is becoming increasingly important for the understanding of population and community dynamics, and the conservation and management of species

(Roughgarden *et al.*, 1988; Rowley, 1989; Fogarty *et al.*, 1991; Shepherd & Brown, 1992; Doherty & Fowler, 1994).

Abalone are dioecious broadcast spawners (Mottet, 1978). Currents can rapidly disperse gametes thus reducing rates of fertilization (Pennington, 1985; Oliver & Babcock, 1992), which may result in low levels of recruitment, provided immigration from neighbouring populations does not occur. Strategies that maximise fertilization rates are therefore important, and include the formation of spawning aggregations, synchronous spawning events and spawning during particular weather conditions (Himmelman, 1975; Breen & Adkins, 1980; Tutschulte & Connell, 1981; Pennington, 1985; Shepherd, 1986b; Prince *et al.*, 1987; Haag & Garton, 1992; Oliver & Babcock, 1992; Stekoll & Shirley, 1993; Sasaki & Shepherd, 1995). Not all species of abalone utilise these strategies and differences may even occur between populations of the same species (Newell *et al.*, 1982; McShane *et al.*, 1986). Many species of abalone spawn asynchronously (i.e. small groups within a population spawn at different times during the spawning period) (Shepherd & Laws, 1974; Tutschulte & Connell, 1981; McShane *et al.*, 1986), thus spreading the settlement and recruitment period over many months. This may have some advantages if favourable conditions vary randomly throughout the year (Newell *et al.*, 1982), but fertilization rates are likely to be lower unless adult densities are high (Joll, 1980). Identifying spawning patterns is therefore important as the timing and mode of reproduction can influence fertilization rates, from which recruitment patterns are ultimately derived.

Abalone produce planktonic lecithotrophic larvae that settle after 4-10 days (Leighton, 1972, 1974; Leighton *et al.*, 1981; Peña, 1984). Events in the plankton can alter the supply of larvae over time and space to settlement areas, potentially causing large variations in recruitment (Tegner & Butler, 1985; Knowlton & Keller, 1986; Young, 1986; Prince *et*

al., 1987; Sutherland, 1990; Borsa & Millet, 1992; Gaines & Bertness, 1992). Early laboratory studies suggested that the larvae entered the water column where they were potentially dispersed tens of kilometres (Yano & Ogawa, 1977; Ebert & Houk, 1984; Hooker & Morse, 1985; McShane *et al.*, 1988). Current field studies suggest that abalone larvae do not enter the water column but remain near the surface of the parental reef (Prince *et al.*, 1987; McShane *et al.*, 1988), or they are concentrated in stagnation zones created by eddies around headlands or submerged reefs (Shepherd *et al.*, 1992). Predictions about recruitment patterns will obviously differ under each hypothesis, which may have important implications for the management of abalone fisheries.

Settlement of abalone is induced when larvae contact crustose coralline algae (CCA) (Morse, D.E. *et al.*, 1979a, 1980; Morse, A.N.C. & Morse, 1984; Shepherd & Turner, 1985; Clavier & Richard, 1986; McShane & Smith, 1988; Moss & Tong, 1992a). Settlement cues are important indicators of food and shelter, necessary for post settlement survival (Levin, 1993), so their distribution may influence patterns of successful recruitment (Sebens, 1983). CCA are abundant on rocky reefs and are therefore an appropriate settlement cue for reef dwelling animals, including abalone (Gee, 1965; Barker, 1977; Heslinga, 1981; Rumrill & Cameron, 1983; Sebens, 1983; Shepherd & Turner, 1985; McShane & Smith, 1988; Pearce & Scheibling, 1990, 1991; Johnson *et al.*, 1991b; McGrath, 1992).

Debate exists as to whether the settlement inducing molecule is produced by the CCA or by bacteria specific to the surface of CCA (Morse, A.N.C. & Morse, 1984; Morse, A.N.C. *et al.*, 1984; Morse, D.E., 1985; Johnson *et al.*, 1991a). Most evidence supports an algal origin, but Johnson *et al.* (1991b) found a positive association between the settlement of *Acanthaster planci* larvae and the presence of bacteria on CCA fragments. A similar

association was not detected with abalone larvae although the results were inconclusive (Johnson *et al.*, 1991a). In the laboratory, abalone will settle in the mucous trails of conspecifics (Seki & Kan-no, 1981). Settlement in response to conspecifics has been observed for many marine species (Burke, 1986), but the natural distribution of newly settled larvae does not support this hypothesis for abalone (Shepherd & Turner, 1985). Despite the lack of evidence for non-CCA associated cues, alternatives should still be considered as not all species of abalone occupy habitats where CCA are abundant.

Recently metamorphosed larvae enter a post-settlement phase before recruiting into the adult population. During this period settlement patterns can be altered by differential mortality between settlement sites and/or post-settlement migration, thus altering local recruitment densities (Morse, D.E. *et al.*, 1979b; Keough & Downes, 1982; Young & Chia, 1982, 1984; Connell, 1985; Peck & Culley, 1990; Stoner, D.S., 1990; McShane, 1992; Osman *et al.*, 1992). Identifying post-settlement processes is therefore important if recruitment patterns are to be used as indicators of settlement patterns (Keough & Downes, 1982; Connell, 1985; Davis, 1988).

In summary, recruitment patterns can vary across time and space due to a range of processes affecting early life history stages. Variable recruitment patterns are important in explaining changing juvenile and adult distribution patterns. Therefore, it is essential to investigate early life history processes if valid conclusions are to be made about the distribution and abundance of a particular species.

1.4 Species Description

Haliotis cyclobates Péron, 1816

Haliotis cyclobates is distinguished by its small size and sub-circular, high spired shell (Plate 1.1). Its shell is sculptured with strongly spiralling threads crossed by collabral

a

b

1cm

Plate 1.1 *Haliotis cyclobates*. **(a)** Mature adult (5+ years) **(b)** Young adult (≈3 years)

folds. The external colour consists of radiating flames of brown, green and cream and the interior is iridescent. The tremata are small, oval and slightly raised, occurring along a spiral located near the margin. Approximately 5-6 tremata are open at a time. Adults can obtain shell diameters of 84 and 66mm with a spire height of 33mm (Cotton, 1959; Ludbrook & Gowlett-Homes, 1989).

The animal is generally dark, particularly along the epipode, which is fringed by fine, pale-green processes extending from the mantle (Cotton, 1959). The sole of the foot is creamy-yellow and frequently ringed by a pale-green band dividing it from the epipode.

It is distributed from western Victoria to southern Western Australia and occurs in sheltered waters. It ranges from the shallow subtidal to 15m, and is frequently associated with seagrass meadows or shells of the bivalve *Pinna bicolor* (Gmelin) (Cotton, 1959; Ludbrook & Gowlett-Homes, 1989).

1.5 Study Site Description

The study was done at Edithburgh, on the Yorke Peninsula, South Australia (35°05'S: 137°40'E). Four sites were selected to the north, northeast, southeast and south of the jetty (Fig.1.1). The average depth for each site was 3m, 6m, 6m and 4m respectively. The north and eastern sites consisted of adjacent seagrass and open areas, but only seagrass was represented at the south site.

Seagrass areas consisted of *Posidonia* spp. beds, with small patches of *Amphibolis* spp. occurring in shallow water. Small patches of hard substrata (e.g. rocks, bottles, and shells of the large bivalve *Pinna bicolor*) provided habitat for *H. cyclobates* in these areas.

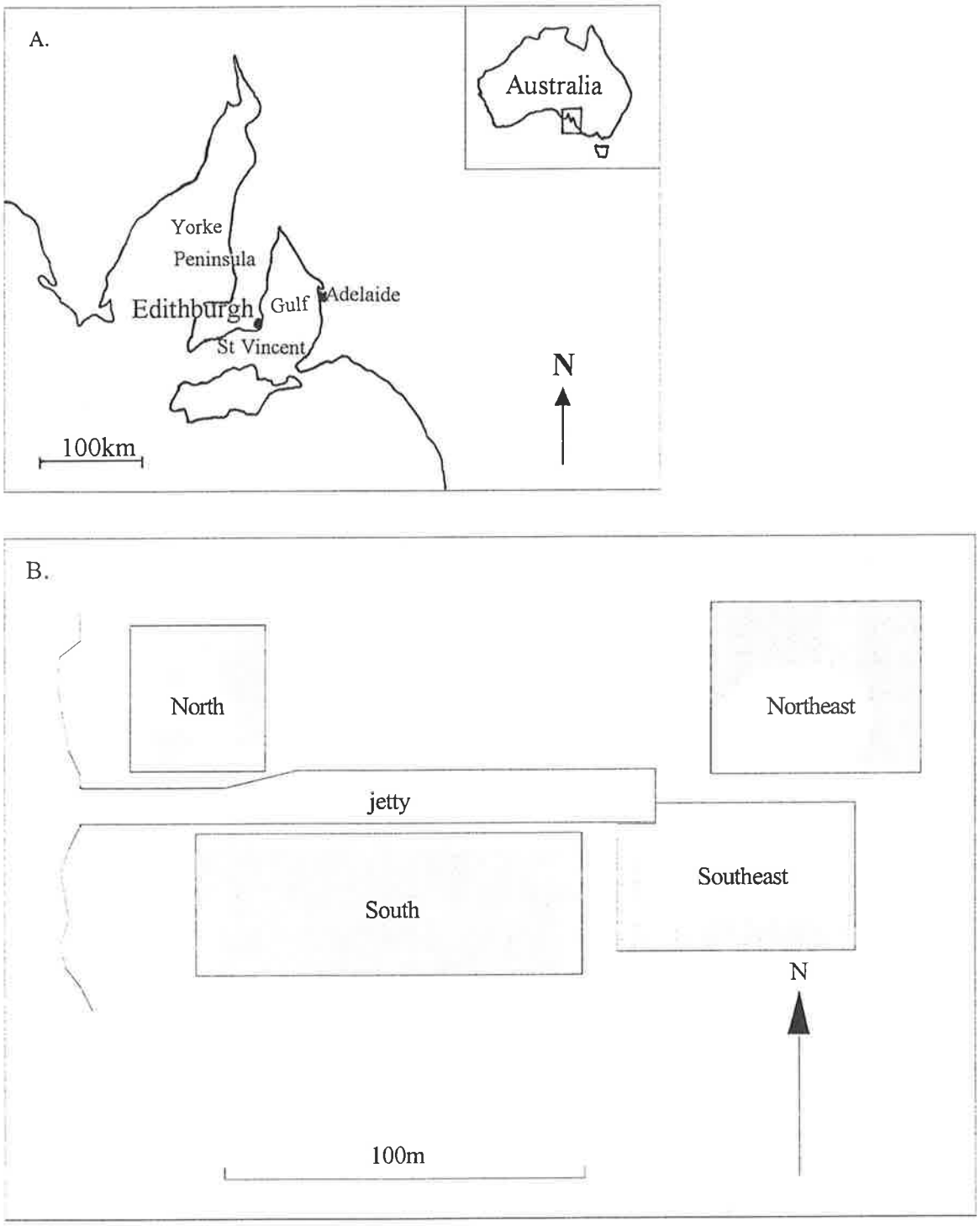

Figure 1.1 **A.** Location of Edithburgh, South Australia. **B.** Diagram of Edithburgh Jetty showing the location of the North, Northeast, Southeast and South study sites, and the distribution of seagrass (stippled) and open (clear) areas within each site.

Open sites were either bare sand with small patches of hard substrata (north site) or areas of patchy sand and small to medium sized calcareous rocks (northeast and southeast sites). Patches of algae and seagrass (*Halophila australis* Daty & Stone) occurred at these sites but did not form extensive beds.

The study site was sheltered except during northeast storms which produced strong swells. These storms disturbed the bottom and transported drifting plant debris (algae and seagrasses referred to as "drift weed" in this thesis) into shallow areas where it accumulated as large mats. Currents were predominantly tidal, flowing north during flood and south during ebb tides. The sea temperature varied between 12°C (winter) and 22°C (summer).

1.6 Study Aims

In the following chapters I will map the local distribution of *H. cyclobates* and investigate the importance of predation, food, shelter and its early life history in determining its distribution. In chapter five I will discuss the results of each chapter, concluding with an assessment of which processes best explain the distribution of *H. cyclobates* at Edithburgh.

CHAPTER 2 DISTRIBUTION & ABUNDANCE

2.0 Introduction

At Edithburgh, *H. cyclobates* is found on patches of hard substrata in vegetated (seagrasses) and unvegetated (open) areas. Differences in the densities of abalone were apparent between the two habitats, so I surveyed the distribution and abundance of *H. cyclobates* in open and seagrass areas to test the hypothesis that more abalone occurred in seagrass areas than in open areas. The results were then used to generate hypotheses about the processes that affect the local distribution and abundance of *H. cyclobates*.

2.1 Materials and Methods

The distribution and abundance of *H. cyclobates* was surveyed in seagrass and open areas at the North, Northeast and Southeast sites (see Fig.1.1). At each site, forty $(0.5m)^2$ quadrats were haphazardly dropped in each habitat and the number of *H. cyclobates* and patches of hard substrata in each quadrat scored. Quadrat locations were determined by blindly swimming 4 to 5m in a random direction and dropping the quadrat into the seagrass. Results were analysed using a two factor ANOVA to determine if abalone and substratum densities were affected by site (3 levels) and habitat (2 levels; seagrass and open). Furthermore, as *H. cyclobates* only occurs on hard substrata, the number of abalone and patches of hard substrata per quadrat were compared to determine if a significant correlation occurred between the two. Error rates were set at α=0.05 and ß=0.2.

2.2 Results

Densities of *H. cyclobates* were higher in seagrass areas than in open areas at the eastern sites, but this pattern was reversed at the North site (Fig.2.1). Statistical analyses were not strictly valid and must be treated cautiously because of unequal variances and non-normal data, even after transforming to logs. However, as is evident from figure.2.1, significant habitat and interaction (site by habitat) effects were detected (Table 2.1). Excluding the North site resulted in only a significant habitat effect (Table 2.2). No significant difference between abalone densities in open and seagrass areas was detected at the North site, despite higher densities being observed in the open area (ANOVA, F=3.176, d.f.=1,78, p=0.08). The power of this test was calculated as P=55%, indicating that the result may represent a type II error.

Table 2.1

Analysis of mean density of *H. cyclobates* in open and seagrass areas at each of three sites at Edithburgh, S.A. The reliability of this test may be suspect due to unequal variances and non-normal data, although n=40 in all cases. α=0.05 and * denotes a significant result.

ANOVA			
Source of Variation	df	MS	*F* ratio
Site	2	0.000	0.000
Habitat	1	2.400	5.341*
S X H	2	3.150	7.010*
Residual	234	0.449	

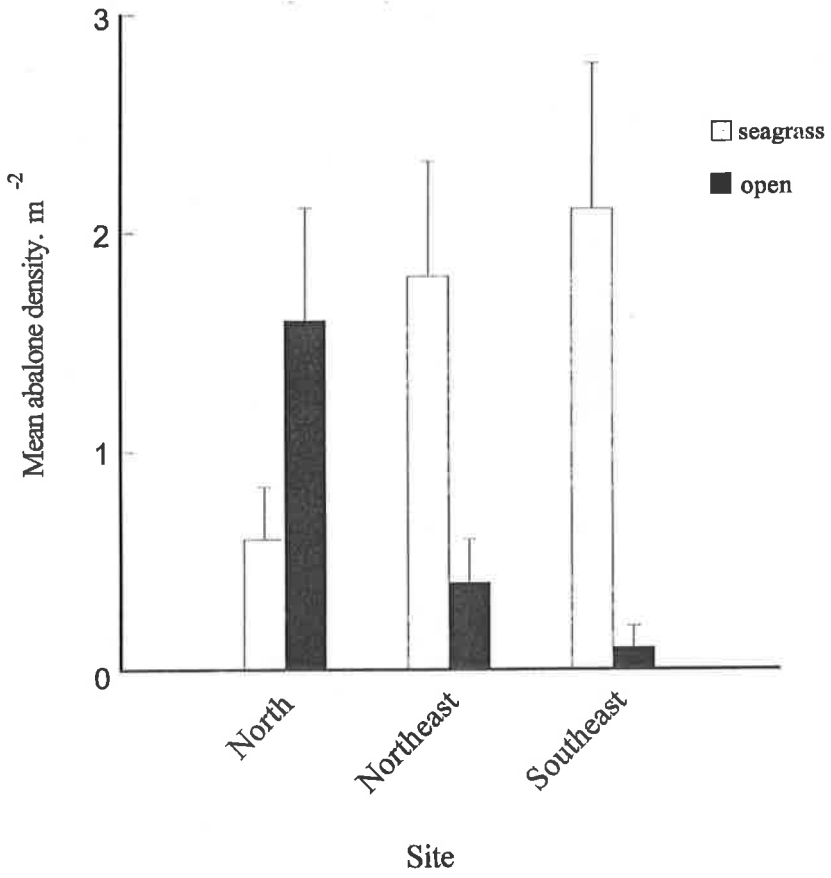

Figure 2.1 Mean density (± SE) of*Haliotis cyclobates* in seagrass and open areas at three sites around Edithburgh jetty.

Table 2.2

Analysis of mean density of *H. cyclobates* in open and seagrass areas at the eastern sites at Edithburgh, S.A. The reliability of this test may be suspect due to unequal variances and non-normal data, although n=40 in all cases. α=0.05 and * denotes a significant result.

ANOVA			
Source of Variation	df	MS	*F* ratio
Site	1	0.000	0.000
Habitat	1	7.225	15.139*
S X H	1	0.225	0.471
Residual	156	0.477	

Densities of substrata varied significantly between sites and habitats (Table 2.3), with higher densities occurring in open areas (Fig.2.2). A two factor ANOVA of the eastern sites indicated a significant habitat effect but no site or interaction effect (Table 2.4). At the North site no significant difference was detected between the substratum densities in open and seagrass areas (ANOVA, F=2.08, d.f.=1,78, p=0.15), although the power of this test was P=41%.

Figures 2.1 and 2.2 suggest a possible negative correlation between abalone density and substratum density. No significant correlation was detected between abalone numbers and the number of hard substrata in each quadrat (Fig. 2.3) (Spearman Rank Correlation, r= 0.408, n=240, p>0.05). I considered this result to be robust because the power of the test was greater than 80% (Cohen, 1988).

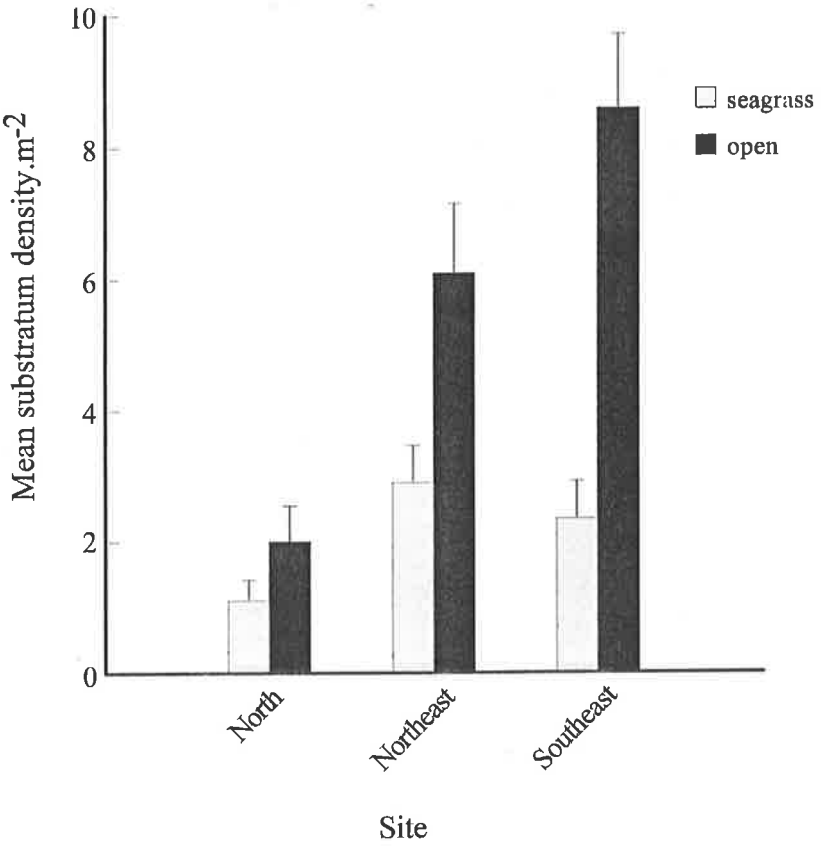

Figure 2.2 Mean density (± SE) of hard substratum in seagrass and open areas at three sites around Edithburgh jetty.

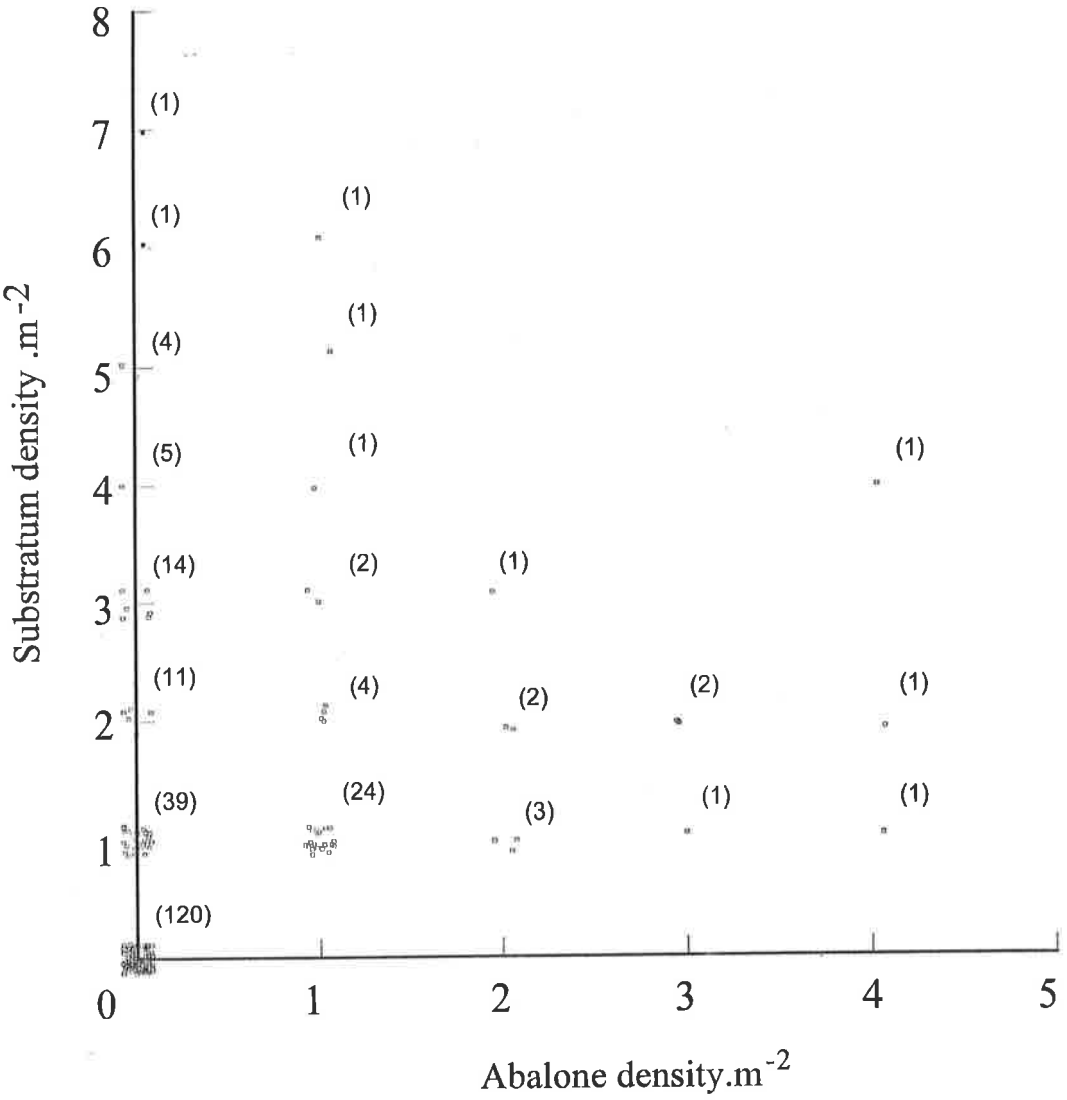

Figure 2.3 The densities of *Haliotis cyclobates* and hard substrata found in each of 240, ($0.5m^2$)quadrats. Numbers in parentheses indicate the number of observations for each co-ordinate. No significant correlation was detected ($r=0.408$, $n=240$, $p>0.05$).

Table 2.3

Analysis of mean density of hard substrata in open and seagrass areas at each of three sites at Edithburgh, S.A. The reliability of this test may be suspect due to unequal variances and non-normal data, although n=40 in all cases. α=0.05 and * denotes a significant result.

ANOVA			
Source of Variation	df	MS	*F* ratio
Site	2	21.088	14.835*
Habitat	1	44.204	31.097*
S X H	2	8.829	6.211*
Residual	234	1.421	

Table 2.4

Analysis of mean density of hard substrata in open and seagrass areas at the eastern sites at Edithburgh, S.A. The reliability of this test may be suspect due to unequal variances and non-normal data, although n=40 in all cases. α=0.05 and * denotes a significant result.

ANOVA			
Source of Variation	df	MS	*F* ratio
Site	1	2.500	1.324
Habitat	1	55.225	29.238*
S X H	1	5.625	2.978
Residual	156	1.889	

CHAPTER 3 FOOD AVAILABILITY AND PREDATION

3.0 Introduction

Seagrass meadows provide food and shelter for a variety of species (Ansari *et al.*, 1991; Irlandi & Peterson, 1991; Rainer & Wadley, 1991; Stoner & Sandt, 1991; Sogard & Olla, 1993). The occurrence of *H. cyclobates* in seagrass meadows at Edithburgh may therefore be due to one or a combination of these factors. Shepherd (1973) found that seagrasses and their epiphytes constituted the bulk of the diet of *H. cyclobates* at Tipara Reef, South Australia; feeding occurred at night and passive foraging was common. When food is abundant many species of abalone cease moving and forage passively (Mottet, 1978), using their foot to trap pieces of weed growing or drifting nearby (Shepherd, 1973). Passive foraging maximises energy intake (Pyke, 1984; Macchiusi & Baker, 1992), so passive foraging within seagrass habitats may represent an optimal foraging strategy for *H. cyclobates*.

Alternatively, seagrass may help protect *H. cyclobates* from predation. *Haliotis cyclobates* occupies small patches of hard substrata that lack cryptic refuges. The structural complexity of seagrass meadows may reduce the searching efficiency of predators (Shepherd, 1973) and, if so, detection by predators may be more likely in unvegetated areas than in seagrass. Predators identified at Edithburgh were gastropods, *Lyria mitraeformis* (Lamarck, 1804) and *Pleuroploca australasia* (Perry, 1811), seastars, *Coscinasterias muricata* (Gray, 1840) and *Uniophora granifera* (Lamarck, 1816), and possibly a crab, *Nectocarcinus integrifrons* (Latreille, 1825). Other predators, such as stingrays, were present but were rarely seen, although damaged shells attributable to

stingray attack were common. Furthermore, *H. cyclobates* crosses patches of sand while actively foraging. Its inability to adhere firmly to soft sediments makes it vulnerable to predation while on sand, unlike passively foraging abalone which can adhere firmly to the hard substratum they are sitting on. Therefore, passive foraging from hard substrata within seagrass meadows may serve to avoid predation.

In this chapter, dietary surveys and two experiments were done to assess the importance of predation and food in determining the distribution of *H. cyclobates* at Edithburgh. Diets were surveyed to assess if seagrass was an important food source and whether more food was consumed per night in seagrass areas than in open areas, predation was examined by experimentally comparing short term survivorship of abalone in open and seagrass areas, and the effect of food on abalone movement was studied to determine if abundant food reduced rates of active foraging.

3.1 Materials & Methods

3.1.1 Diet

3.1.1.1 Proportion of Seagrass in Diet

The proportion of seagrass in the diet of *H. cyclobates* was determined by examining the gut contents of abalone collected from two sites, each with an open and seagrass area. Ten abalone, five from each habitat, were collected from each site. Collections were made in the morning so stomach contents could be fixed before extensive digestion of the previous night's food occurred. The sites were not sampled at the same time but approximately three weeks apart during September and October, 1993. Possible temporal variations between sites were not considered as no direct comparisons between sites were made; the

aim was only to estimate the amount of seagrass in the diet, relative to other foods, at each site.

Abalone were dissected and the visceral mass preserved in 10% seawater-formalin for one week to harden soft tissues. Stomach contents were collected by opening the crop and the stomach and scraping and flushing out all loose material. This material represented food consumed the previous night and was the least digested, thus minimising biases associated with under or overscoring food fragments due to their digestibility.

The stomach contents were examined under a low power dissecting microscope and sorted into three groups, 1) seagrasses, 2) red algae and, 3) other fragments (consisting mostly of unidentifiable fragments). The total dry weight (organic and inorganic) of each sample, for each abalone, was obtained by drying the samples at 60°C for two days. Samples were then placed in a 250°C oven for two days to remove organic material. Organic dry weights were then calculated for each sample by subtracting inorganic dry weights from total dry weights. For each abalone total organic dry weights could then be calculated and the organic dry weight of each group expressed as a percentage of this total. The mean and standard error of the percentage of seagrass was calculated for each habitat within each site. Using these values and with reference to previous studies on the diets of abalone, including *H. cyclobates*, an assessment of the importance of seagrass in the diet of *H. cyclobates* at Edithburgh was made. This form of assessment is subjective, but without analysis of the energy content of seagrass and its epiphytes, and the availability of that energy to *H. cyclobates*, an analytical assessment can not be made.

3.1.1.2 Comparison of the Amount of Food Eaten by Abalone in Open and Seagrass Habitats

To compare the amount of food eaten by abalone in open and seagrass habitats, ten abalone, five from each habitat, were collected from each of the north, northeast and southeast sites. A second collection was made at the north site two days after the first collection, resulting in a total of four sample groups. The total dry organic weight of stomach contents was obtained for each abalone as described above, except that the stomach contents were not separated into three groups. Furthermore, within each site, abalone collected from both habitats were all within the same size class. Differences in the size structure of abalone between sites prevented the same size class being collected from all sites. At each site a t-test, comparing the mean organic dry weights of stomach contents obtained for each habitat, was done to test the hypothesis that the amount of food eaten by abalone in one night did not differ significantly between open and seagrass habitats. Comparisons between sites were not done because the size classes varied between sites and the amount eaten may vary with size. Power was calculated with respect to detecting a 20% difference between means and error rates for the t-tests were set at α=0.05 and ß=0.20.

3.1.2 Predation

Predation is a principal cause of mortality amongst abalone (Mottet, 1978; Hines & Pearse, 1982; Shepherd, 1990). Therefore I assumed predation to be the greatest source of short term mortality and, by measuring survivorship, I tested the hypothesis that mortality due to predation did not differ between open and seagrass habitats.

To compare survivorship, six areas, three each in seagrass and open areas, were chosen, and one 3m x 3m plot was staked out in each area. Plots were spaced 10m-30m apart to minimise placement effects caused by clumping the replicate plots.

For each plot thirty adult *H. cyclobates* (shell length >30mm) were collected from the surrounding area and returned to the laboratory for tagging. Abalone were collected from seagrass and open areas. Abalone were tagged by cleaning and drying the back of the shell and then fixing a coloured, numbered tag to the shell with a quick drying, two part epoxy resin. Animals were randomly assigned to each plot in the laboratory and kept overnight in six groups of thirty in glass aquaria filled with aerated, natural seawater.

Animals were released by gently holding them against appropriate substrata in the plots until they gripped with the foot. After six and eighteen days the plots were searched to determine survivorship.

Results were recorded by thoroughly searching hard substrata inside, and for 5m around, each plot for living and dead abalone. Dead abalone were determined by the recovery of empty, tagged shells. Any abalone not found were classed as missing. Results were structured as contingency tables and Fisher's Exact test in the package STATXACT^{TM} was used to test the null hypothesis that the proportion of living abalone did not differ between plots or between habitats. Error rates were set at α=0.05 and β=0.20.

3.1.3 Food Abundance

To investigate the effect of food on the foraging behaviour of *H. cyclobates*, I tested the null hypothesis that the frequency of movement was independent of the presence of food.

Abalone were assigned to one of three treatments and their behaviour scored after one

night. The treatments were; 1) bare - abalone placed on a suitable patch of hard substratum but no food supplied, 2) food - as above but patch supplied with food and 3) shelter - abalone placed on a patch and supplied with an inedible mimic of the food. The food was supplied as a bunch of seagrass and algae attached to a small rock with a rubber band. It consisted mostly of the seagrass *Posidonia* sp. and a filamentous red alga, both of which were readily eaten by *H. cyclobates* (pers. obs.). The shelter treatment was included to differentiate between a food or shelter response, either of which may have induced the abalone to remain near the food treatment. The shelter treatment was a group of green plastic strips tied so as to mimic the food treatment and attached to a small rock with a rubber band.

Three experimental plots were established, one at the North site and two at the Southeast site. Each plot was $(5m)^2$, and divided into a $(0.5m)^2$ grid. Plots were labelled deep-sand, deep-rubble and shallow-sand according to depth and substratum characteristics.

From the surrounding area forty five abalone, on small, transportable substrata (e.g. *Pinna* shells and bottles), were collected for each plot, and each treatment was randomly assigned 15 abalone. Treatments were randomly distributed on the grid, which maintained a minimum distance of 0.5m between treatments. Substrata with abalone that were assigned to the food or shelter treatments were positioned so that the abalone were in direct contact with the plant material or plastic strips. The use of small transportable substrata reduced handling stress on the abalone. Individual abalone were distinguished by recording the epiphyte patterns on their shells. Although time consuming, this method avoided handling the abalone and was sufficient for the short duration of the experiment.

Three trials were done on the deep-sand plot and seven on the shallow-sand plot during February 1994. Six trials were done on the deep-rubble plot between November 1993 and

February 1994. *Haliotis cyclobates* is nocturnal so trials were run overnight, and the results scored the next morning by recording, for each treatment, how many abalone had remained on or moved from the experimental patches they had been assigned to. Results were analysed for homogeneity between trials within plots using heterogeneity log-likelihood tests, while pooled within-plot data were tested for treatment effects as 3x2 or 2x2 contingency tables, using Fisher's Exact test in the package STATXACT^{TM}. Plots were compared using pooled values for the bare and food treatments in a 3 way contingency table using chi-squared test. Error rates for all tests were set at α=0.05 and β=0.20.

3.2 Results

3.2.1 Diet

3.2.1.1 Proportion of Seagrass in Diet

Seagrass fragments were found in 95% of the abalone examined. Fragments were almost exclusively from *Posidonia* spp., with occaisional fragments of *Halophila australis.* The mean percentages of seagrass found in abalone were 33±10% and 24±6% from the seagrass areas, and 15±10% and 13±4% from the open areas. Only two animals, both from the same open area, had consumed measurable quantities of red algae, comprising 3% and 58% of their gut contents. The remaining material was unidentifiable.

3.2.1.2 Comparison of the Amount of Food Eaten by Abalone in Open and Seagrass Habitats

I detected no significant differences between the amounts of organic material found in abalone collected from open and seagrass habitats at any of the sites (Table 3.1). The

power to detect a 20% difference in means was less than 80% in all tests (Table 3.2), and since the observed effect size at the northeast and southeast sites was close to or greater than the effect size required for a 20% change in means, it is probable that the non-significant results obtained for these sites represents a type II error. The observed effect sizes for the north site samples were considerably less than those required for a 20% change, so, although the power was low, I do not consider there to have been a difference in the amount eaten between habitats at this site.

Table 3.1. Results of t-tests comparing mean dry organic weight of stomach contents collected from abalone from open and seagrass habitats at three sites near Edithburgh Jetty. *One sample from the open habitat was lost during processing.

Site	Habitat	mean(±s.e)	t	d.f.	P
North	seagrass	0.022g±0.003g	0.846	8	0.422
	open	0.018g±0.003g			
Northeast	seagrass	0.089g±0.008g	0.229	8	0.824
	open	0.087g±0.010g			
Southeast	seagrass	0.042g±0.010g	1.604	8	0.147
	open	0.062g±0.008g			
North	seagrass	0.040g±0.005g	0.338	7*	0.745
	open	0.042g±0.003g			

Table 3.2 Effect sizes (d) and power of tests available for detecting 20% difference in mean organic material consumed by abalone in open and seagrass habitats. Observed effect sizes (d) are also presented.

Site	$(d)_{20\% \text{ change}}$	$\text{Power}_{20\% \text{ change}}$	Obs. (d)
North	1.00	0.56	0.17
Northeast	0.63	0.26	0.57
Southeast	0.37	0.11	0.87
North	0.80	0.39	0.20

3.2.2 Predation

After six days, no significant differences in the number of living, dead or missing abalone were detected between plots for either habitat (Fisher's Exact test; Seagrass, Fisher statistic = 5.357, d.f.=4, p=0.222; Open, Fisher statistic = 6.255, d.f.=4, p=0.119). Analysis of pooled values, (Table 3.3), found no significant difference between habitat-types in the number of abalone found alive, dead and missing, indicating that survivorship was equal (Fisher's Exact test, Fisher statistic = 2.693, d.f.=2, p=0.264). The observed effect size was w = 0.12, which can be considered a small effect (Cohen, 1988). It was deemed negligible because differences were mainly due to more abalone scored missing from seagrass plots than from open plots, a result probably caused by the seagrass canopy inhibiting the detection of abalone that had dispersed from the plots.

Table 3.3. Survivorship of *H. cyclobates* in each of 2 habitats after 6 days. Values are pooled across 3 plots for each habitat.

	Alive	Dead	Missing	Total
Seagrass	58	4	28	90
Open	68	3	19	90
Total	126	7	47	180

A similar pattern of survivorship was observed after 18 days (Table 3.4), despite a large increase in the number of abalone missing from both habitats. However, significant variation between open plots (Fisher's Exact test, Fisher statistic = 14.79, d.f.=4, p=0.005), mostly due to a difference in missing abalone (Table 3.5), precluded appropriate analysis between habitats. The presence of a similar number of dead shells in each habitat (Table 3.4) suggests that survivorship did not differ between the two habitats.

Table 3.4. Survivorship of *H. cyclobates* in each of 2 habitats after 18 days. Values are pooled across 3 plots for each habitat.

	Alive	Dead	Missing	Total
Seagrass	25	7	58	90
Open	36	8	46	90
Total	61	15	104	180

Table 3.5. Survivorship of *H. cyclobates* in each of 3 open areas after 18 days. Variation between plots is mostly due to differences in the numbers of missing abalone.

	Alive	Dead	Missing	Total
Plot 1	6	2	22	30
Plot 2	13	1	16	30
Plot 3	17	5	8	30
Total	36	8	46	90

3.2.3 Food Abundance

3.2.3.1 Deep-sand plot

Trials were not significantly heterogeneous (Log-Likelihood test for heterogeneity of trials, G = 2.042, d.f.= 4, p>0.05) so pooled results were compared (Table 3.6). The ratio of the number of abalone present to the number absent was found to differ significantly between treatments (Fisher's Exact test, Fisher statistic = 10.030, d.f.=2, p = 0.007), so the table was broken down into 2x2 tables to determine where the differences lay. The presence to absence ratios did not differ significantly between the bare and shelter treatments (Fisher's Exact test, Fisher statistic = 2.848, d.f.= 1, p =0.137), so they were pooled and compared to the food treatment. I found that significantly more abalone remained in the food treatment than the (bare+shelter) category (Fisher's Exact test, Fisher statistic = 7.189, d.f.=1, p=0.01).

Table 3.6. The number of *H. cyclobates* present and absent in each of 3 treatments in the deep-sand plot. Values represent pooled data from trials 1 - 3.

	Bare	Food	Shelter	Total
Present	24	31	16	71
Absent	21	14	29	64
Total	45	45	45	135

3.2.3.2 Deep-rubble plot

The six trials were not significantly heterogeneous (Log-Likelihood test for heterogeneity of trials, G = 10.917, d.f.=10, $p>0.05$) so data were pooled (Table 3.7). The ratio of the number of abalone present to the number absent was found to differ between treatments (Fisher's Exact test, FI = 20.38, d.f.=2, $p<0.001$), so the table was broken down into 2x2 tables to determine differences. No significant difference was detected between the bare and shelter treatments (Fisher's Exact test, Fisher statistic = 0.177, d.f.=1, $p=0.739$), so they were pooled and compared to the food treatment. I found that significantly more abalone remained in the food treatment than in the pooled category (Fisher's Exact test, Fisher statistic = 20.358, d.f.=1, $p<0.001$).

Table 3.7. The number of *H. cyclobates* present and absent in the deep-rubble plot in each of 3 treatments. Values represent pooled data for trials 1 - 6.

	Bare	Food	Shelter	Total
Present	26	50	23	99
Absent	65	40	66	171
Total	91	90	89	270

3.2.3.3 Shallow-sand plot

All trials were not significantly heterogeneous (Contingency Log-Likelihood test for heterogeneity of trials, G = 6.813, d.f = 12, p>0.05), and a significant difference in the ratio of abalone remaining to absent was detected when the pooled data, (Table 3.8), were analysed (Fisher's Exact Test, Fisher statistic = 13.34, d.f. = 2, p = 0.001). After dividing the table into 2x2 tables I found no significant difference between the bare and shelter treatments (Fisher Exact test, Fisher statistic = 2.850, d.f.= 1, p = 0.112), so they were pooled. Comparing the pooled data to the food treatment, I found that significantly more abalone remained in the food treatment (Fisher Exact test, Fisher statistic = 10.292, d.f.=1, p=0.002).

Table 3.8. The total number of *H. cyclobates* present and absent in each of three treatments in the shallow-sand plot. Values represent data pooled across seven trials.

	Bare	Food	Shelter	Total
Present	77	92	85	254
Absent	25	6	15	46
Total	102	98	100	300

3.2.3.4 Power of the bare - shelter tests

I found that the power for each of the non-significant Fisher Exact tests comparing the bare and shelter treatments was less than 80%, (Deep-sand, 41%; Deep-rubble, 7%;

Shallow-sand, 40%). These values reflect the effect size values of w = 0.179, w = 0.032, and w = 0.121 respectively (Cohen, 1988). Therefore, whether these values represent negligible differences between treatments or a Type II error is unknown, although from *insitu* observations of the foraging behaviour of *H. cyclobates* I would expect the availability of food and not the presence of shelter to be the major factor determining movement.

3.2.3.5 Comparison between plots

Plots were compared to determine whether the responses to the bare/shelter and food treatments were equal across plots (Table 3.9). I combined the shelter treatment with the bare treatment because no significant differences were found between these treatments. Plots were compared using a 3 way contingency table chi squared test with the variables plot (p_n=3), treatment (t_n=2) and result (r_n=2) (i.e. present vs absent) (Zar, 1984). The three variables were not mutually independent (c^2 = 252.066, d.f.= 7, $p<0.05$), and tests for partial independence found significant differences in all comparisons (Table 3.10), indicating that the ratio of abalone present to absent was dependent on treatment and plot effects. The treatment effect reflects the food response already described for each plot and will not be considered here. Pairwise comparisons of plots, testing the hypothesis that plots are independent of (result & treatment), detected significant differences in the presence - absent ratios between all plots (Table 3.11). These differences are probably due to the high proportion of abalone remaining in both treatments in the shallow-sand plot compared to the other plots, and the proportionally greater dispersal of abalone from the bare treatment in the deep-rubble plot than in the deep-sand plot (see Table 3.9).

Table 3.9. The total number of *H. cyclobates* present and absent in the bare/shelter (denoted as bare) and food treatments in each plot. Values represent pooled data from all trials for each plot. Shelter values have been pooled with bare values as no significant differences were found between these treatments.

	Plots					
	Deep-sand		Deep-rubble		Shallow-sand	
	Bare	Food	Bare	Food	Bare	Food
Present	40	31	49	50	162	92
Absent	50	14	131	40	40	6

Table 3.10. Tests for partial independence between the variables result, treatment and plot, in order to determine whether the ratio of abalone present to absent was affected by treatment and/or plot effects.

H_o under test	χ^2 value	d.f.	Probability
Result is independent of (treatment and plot)	172.434	5	$p<0.05$
Treatment is independent of (result and plot)	50.957	5	$p<0.05$
Plot is independent of (result and treatment)	174.170	5	$p<0.05$

Table 3.11. Results of 2x2 comparisons between plots, testing whether the significant plot effect detected in table 3.10 was caused by one or several plots. Chi-squared values represent results of partial independence tests for the H_o that plots are independent of (results and treatment) for each plot combination.

Pair Combination	χ^2 value	d.f.	Probability
Deep-sand vs Deep-rubble	10.276	3	$p<0.05$
Deep-sand vs Shallow-sand	53.334	3	$p<0.05$
Deep-rubble vs Shallow-sand	145.320	3	$p<0.05$

CHAPTER 4 SETTLEMENT & RECRUITMENT

4.0 Introduction

Haliotis cyclobates appears to be adapted to seagrass areas (Shepherd, 1973) so its early life history may be suited to maximising recruitment in this habitat.

Like many species of abalone, *Haliotis cyclobates* spawns synchronously (Shepherd & Laws, 1974). New recruits (shell length less than 10mm) have, however, not previously been detected. Juveniles of other abalone in this size range are regularly found on crustose coralline algae (CCA), so the absence of *H. cyclobates* juveniles is surprising if CCA is their preferred settlement substratum. In seagrass meadows at Edithburgh CCA occur mostly as small isolated crusts on seagrasses or hard substrata (pers. obs). CCA may therefore not be a suitable settlement cue for *H. cyclobates*. Instead, settlement may occur preferentially on a substratum associated with seagrass areas or non-preferentially on a variety of substrata, followed by post-settlement processes that result in recruitment being highest in seagrass areas.

In this chapter I examine the spawning cycle, settlement substrata and recruitment distribution of *H. cyclobates* at Edithburgh, and discuss how these might influence adult distributions and abundances. The spawning cycle was recorded to determine how reproductive behaviour may contribute to recruitment patterns. The settlement substrata and recruitment distribution were investigated to determine whether preferential settlement or post-settlement processes could explain the distribution of older juveniles and adults.

4.1 Materials & Methods

4.1.1 Spawning

4.1.1.1 Gonad Indices

The reproductive cycle was monitored by estimating gonad indices, which give a relative measure of gonad bulk (Mottet, 1978). Maturing gonads are indicated by increasing values and decreasing values indicate spawning periods. I calculated gonad indices using the method described by Shepherd and Laws (1974).

Five to ten adults were collected from seagrass areas every one to two months, between August 1992 and December 1993. Samples were hardened by storing them in 10% seawater-formalin for one week. The conical organ was sectioned near its base (Fig.4.1), and the outlines of the gonad and digestive gland were traced onto plastic film. Tracings were transferred to paper, cut out and weighed. Gonad indices were then calculated according to the following formula:

$$\text{Gonad Index (G.I.)} = \frac{\text{(weight of gonad cutout)}}{\text{(total weight of gonad and digestive gland cutouts)}}$$

The sexes were not separated and the mean and standard error for each sample was calculated and plotted against time.

4.1.1.2 Weather Conditions

Data for air temperature, wind speed and wind direction were obtained for November 1993 from the Australian Bureau of Meteorology. The data were used to determine

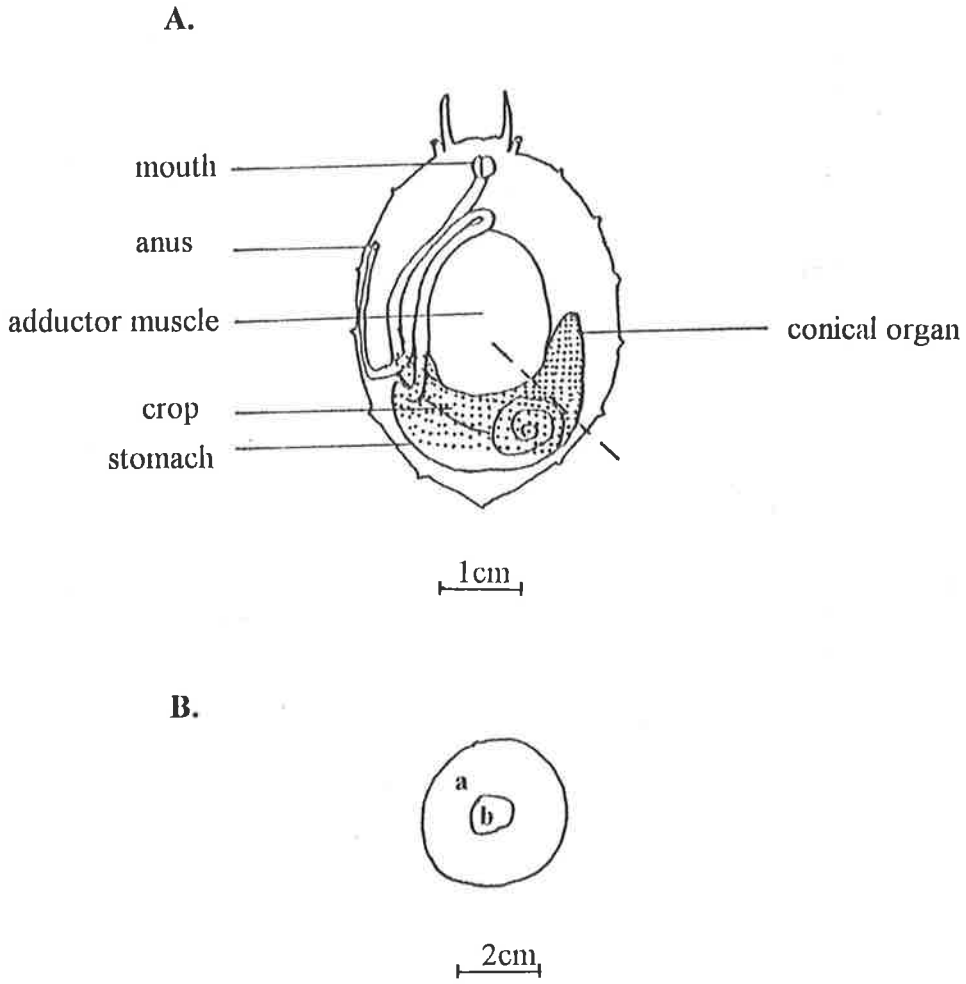

Figure 4.1 **A.** Dorsal view of *Haliotis cyclobates*, (shell removed) Dashed line represents the point where the conical organ was sectioned to obtain gonad samples. Hatched area indicates area covered by gonad in a reproductively mature adult.
B. Transverse section through the conical organ of a reproductively mature abalone, showing the gonad (a) surrounding the digestive gland (b)

whether any periods of calm weather (see Breen & Adkins, 1980; Prince *et al.*, 1987; McShane, 1992) or rough weather (see Sasaki & Shepherd, 1995) could be correlated with the onset of spawning by *H. cyclobates* detected during November (see Results).

4.1.2 Settlement

4.1.2.1 Surveys

Collections of hard and other substrata were made around Edithburgh jetty and searched for newly settled recruits (shell length less than 5mm). Samples were initially collected by removing all types of hard substrata from randomly dropped $(0.5m)^2$ quadrats. Later surveys used a $(1m)^2$ quadrat. Samples were washed in dilute alcohol or fresh water and the resulting sediments passed through 1mm, 750µm and 250µm mesh sieves. Sample fractions were then searched for new recruits.

Ten samples of hard substrata were collected from a $(10m)^2$ seagrass area in February 1993. Further samples were collected during the 1993/94 settlement season which also included collections of the seagrass *Posidonia* spp. Seagrass was initially collected by removing all blades from a $(0.5m)^2$ quadrat. Later samples were collected by removing all seagrass blades from a 3m x 0.2m rectangular quadrat. Blades were cut at their base and placed in a plastic bag for transport to the laboratory. Blades were washed and samples collected as described for hard substrata. In total, during the 1993/1994 settlement season, 23 samples of seagrass and 23 samples of hard substrata from amongst seagrass were collected using $(0.5m)^2$ quadrats and 24 samples of seagrass and 14 samples of hard substrata from amongst seagrass were collected using the later methods. Five samples of hard substrata, cleared from $(1m)^2$ quadrats, were also collected from an open area.

4.1.2.2 Settlement Preference Experiment

An attempt was made to determine the preference of settling *H. cyclobates*. Four types of substrata, CCA, bare rock, shell fragments and glass, were used. Apart from CCA all substrata were common in the study area and adult and juvenile *H. cyclobates* were regularly found on each type. Glass occurred as bottles thrown from Edithburgh jetty. CCA was obtained by transferring small CCA covered boulders from a nearby rocky reef to the study area.

Substrata were laid in square patches, arranged in a Latin square design. Each substratum patch was $(0.5m)^2$ and separated from neighbouring patches by 0.5m. Two $(4.5m)^2$ Latin squares, 5m apart, were established in open areas in 6m of water. The squares were set up in early November 1992. In February 1993, approximately 1-2 months after spawning had finished, all substrata from a patch were placed into a plastic bag and taken to the laboratory. Collected substrata were rinsed in dilute alcohol to remove animals which were caught on a 500μm mesh sieve. Using a microscope, samples were searched for new recruits (abalone of shell length less than 5mm).

4.1.2.3 Abundance of Crustose Coralline Algae on Seagrass

Estimates of percentage cover of CCA on seagrass blades were made at two sites around Edithburgh jetty during November 1994. Thirty complete blades were randomly selected from each of the Northeast and South sites and the total surface area and area covered by CCA calculated for each blade. Seagrass blades were rectangular, so the area covered by

CCA was calculated by summing the total length of sections dominated by CCA and multiplying by the blade width. The coverage of CCA was then expressed as a percentage of the total surface area and the mean and standard deviation of percentage cover calculated for each site.

4.1.3 Recruitment

4.1.3.1 Recruitment Period

I collected size-frequency data in order to map periods of recruitment to the adult habitat. Nine surveys were done in a seagrass area south of the jetty, between March 1993 and March 1994. Data were obtained by slowly swimming through the area and measuring (to the nearest millimetre) the long axis of all abalone found. Patches of hard substrata were thoroughly searched for *H. cyclobates*. This method was sufficient to detect abalone less than 5mm. The search time varied between surveys although a minimum of 100 abalone were measured during each survey. Length measurements were sorted in five millimetre size classes and plotted as size-frequency histograms.

4.1.3.2 Spatial Distribution of Recruitment

The recruitment distribution of zero year class juveniles was assessed in 1994. Size-frequency surveys were done in open and seagrass habitats at each of the North and Northeast sites during January 1994 and repeated in March 1994. Data were recorded using the method described above, although fewer than 100 abalone were measured on three occasions.

4.2 Results

4.2.1 Spawning

4.2.1.1 Gonad Indices

Haliotis cyclobates commenced spawning during late spring in 1992 and 1993 (Fig.4.2). In 1993, a major spawning episode commenced between the 4th and 17th of November. In both years the mean gonad index declined rapidly to zero between November and January. This was interpreted as evidence of synchronised spawning in this population. Gonad maturation occurred during winter and peaked in September and October in both years.

4.2.1.2 Weather Conditions

Two, three day periods of calm weather occurred between the 4th and 17th of November (Table 4.1). The first was between the 4th to the 6th and the second was between the 12th to the 14th. Winds were generally less than 15 knots and blowing off the land from the northwest to west, resulting in flat seas. No periods of rough weather occurred, as winds from the northeast occurred only on four days and were 15 knots or less. The maximum air temperature varied between 18 and 31^{o}C.

4.2.2 Settlement

4.2.2.1 Surveys

A total of 12 new recruits (shell length less than 3mm) were found (Table 4.2) & (Plate 4.1). Eleven were from seagrass samples and one from a hard substratum collected from amongst seagrass.

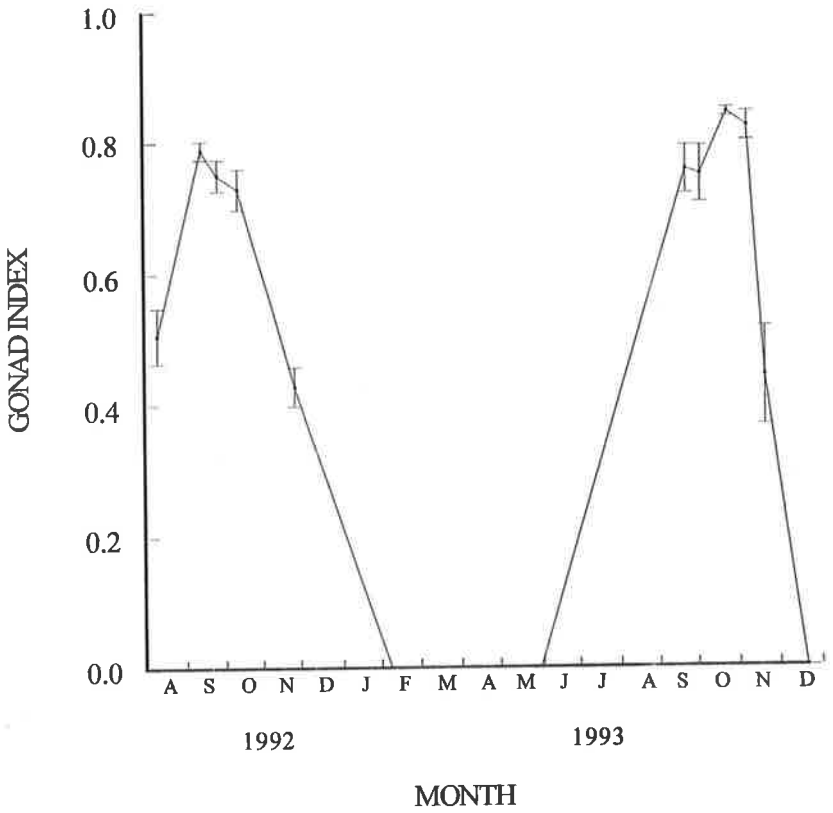

Figure 4.2 Plot showing the seasonal change in mean gonad index (± SE) of *Haliotis cyclobates* at Edithburgh. Declining values represent spawning periods.

Table 4.1 Weather data recorded at Edithburgh Automatic Weather Station for the period 4.11.93 to 17.11.93. Data supplied by the Australian Weather Bureau. Shaded areas represent calm periods at Edithburgh Jetty, as determined by either wind direction or speed. Periods of northeasterly winds are indicated in bold italicised type.

	Daily Temperature (°C)		Wind Direction (degrees)		Wind Speed (Knots)	
Date	Min.	Max.	0900h	1500h	0900h	1500h
4.11.	**9.4**	**18.0**	**210**	**240**	**14**	**13**
5.11.	**12.1**	**20.0**	**300**	**230**	**5**	**9**
6.11.	**7.0**	**21.0**	**350**	**240**	**5**	**15**
7.11.	14.3	19.0	120	100	11	11
8.11.	14.8	18.0	160	170	16	15
9.11.	13.1	19.0	110	140	16	17
10.11.	***14.7***	***23.0***	***70***	***110***	***15***	***12***
11.11.	***16.3***	***33.0***	***40***	***50***	***15***	***9***
12.11.	**15.3**	**22.0**	**300**	**220**	**11**	**15**
13.11.	**11.3**	**22.0**	**300**	**240**	**4**	**17**
14.11.	**12.6**	**22.0**	**120**	**140**	**6**	**9**
15.11.	15.5	21.0	110	160	12	15
16.11.	***16.1***	***23.0***	***80***	***140***	***7***	***9***
17.11.	***15.8***	***31.0***	***40***	***220***	***7***	***16***

4.2.2.2 Settlement Preference Experiment

No new recruits were found on any of the substrata. This suggests either inappropriate siting of the experiment or that inappropriate substrata were used.

Table 4.2 Sizes of newly settled *H. cyclobates* found at Edithburgh during the 1993/94 settlement season.

	Size (mm)	Substratum	Date Found
1	0.80	seagrass	4.11.93
2	1.00	seagrass	"
3	0.85	seagrass	1.12.93
4	1.13	seagrass	"
5	1.54	seagrass	"
6	2.00	seagrass	"
7	2.10	seagrass	"
8	2.41	rock	"
9	1.28	seagrass	18.12.94
10	2.67	seagrass	"
11	2.00	seagrass	18.1.94
12	2.00	seagrass	9.2.94

4.2.2.3 Abundance of Crustose Coralline Algae on Seagrass

The mean percentage cover (± standard deviation) of CCA on seagrass was 12.6 ± 8.77% and 19.77 ± 12.06% from the Northeast and South sites respectively. The percentage cover varied considerably at both sites (N.E. site, min.=0%, max.=27%; South site, min.=0%,

max.=47%), and patches of CCA were only found on old growth sections near the tip of each blade. Other fouling organisms were common and frequently overgrew patches of CCA. Only those patches of CCA that were free of epiphytes contributed to the above results.

4.2.3 Recruitment

4.2.3.1 Recruitment Period

Zero year class recruits (shell length <10mm) were found from March to October 1993 and in March 1994 (Fig.4.3). During 1993 the peak recruitment of the 5-9mm size class occurred in April, followed by a steady decline up to October when no more were found. The reappearance of 5-10mm juveniles in March 1994 indicates a single summer breeding period for this population.

4.2.3.2 Spatial Distribution of Recruitment

Recruitment was detected at all sites during March 1994 but only one juvenile, shell length less than 5mm and found on hard substrata amongst seagrass at the North site, was recorded in January 1994 (Fig.4.4). Recruitment was similar in each area except the Northeast open site, where only one recruit was found. Recruitment was lower, however, in these areas than in the South seagrass site for the same period (see Fig.4.3.i).

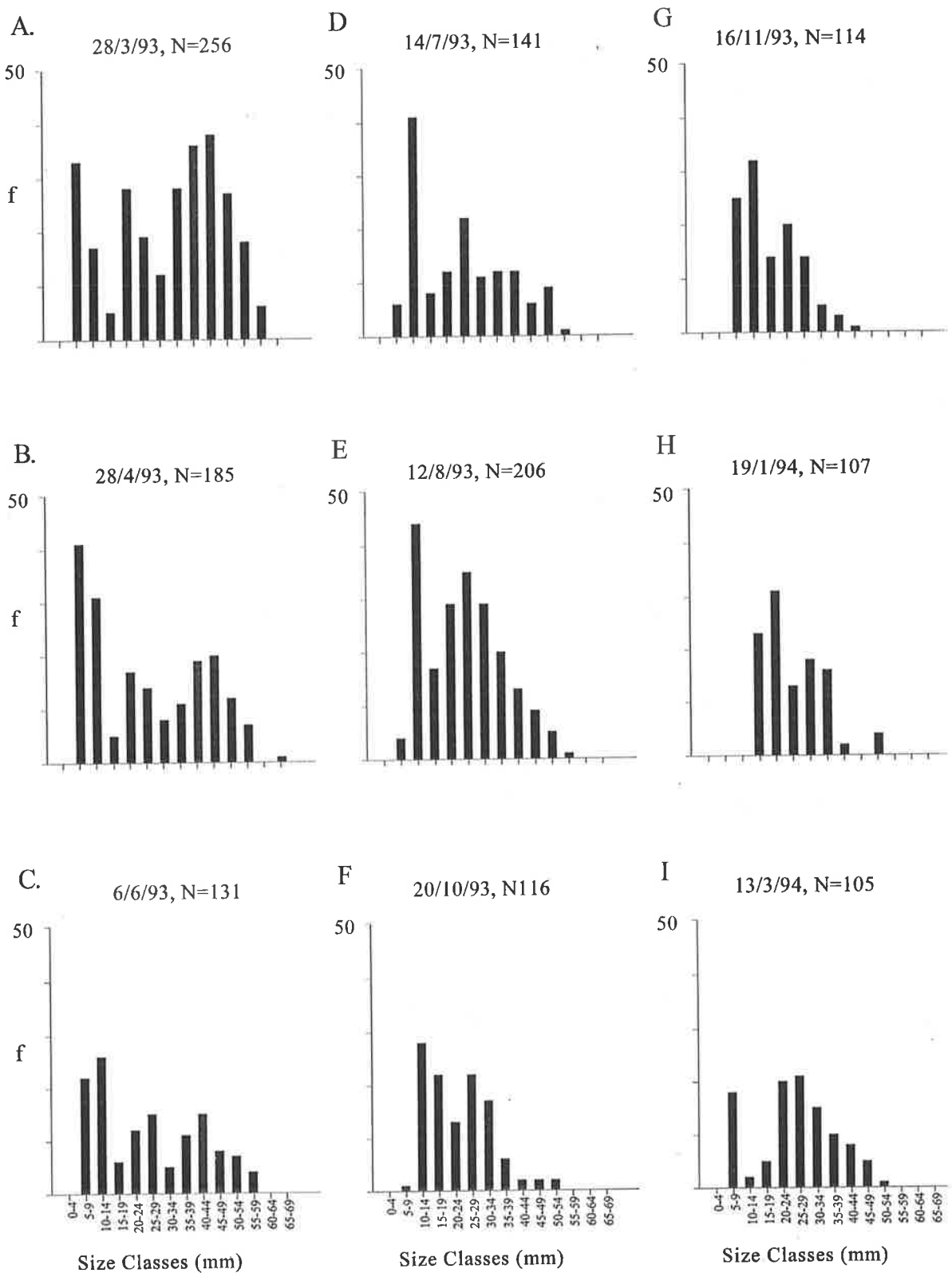

Figure 4.3 Recruitment period of *Haliotis cyclobates*, as indicated by size-frequency surveys taken at the south site between 28.3.93 and 19.3.94. Zero year class recruits are represented by animals in the 0-9mm size class.

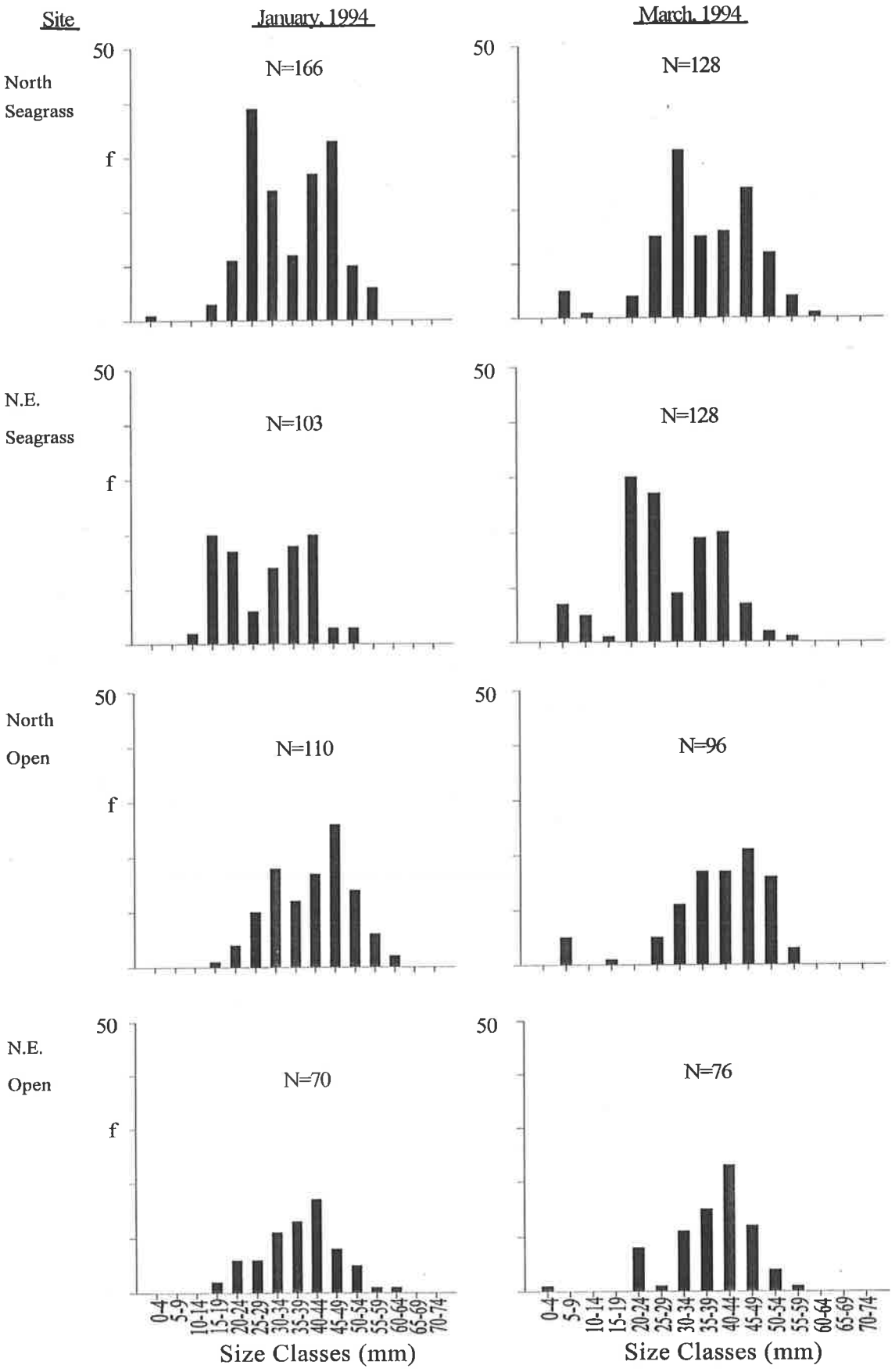

Figure 4.4 Size - frequency distribution of *Haliotis cyclobates* in seagrass and open areas, indicating spatial distribution of recruitment during January and March 1994.

CHAPTER 5 DISCUSSION

5.0 Distribution & Abundance

At Edithburgh, *H. cyclobates* appears to be predominantly distributed on hard substrata within seagrass meadows. Although adjacent open areas had apparently suitable substrata, they were not readily occupied by abalone. The reversal of the pattern at the North site is very interesting because it indicates that open areas can support high densities of abalone. Identifying the factors that enable *H. cyclobates* to occupy this area may therefore be important in explaining its local distribution.

Shepherd (1973) suggests that predation would be the main factor affecting the distribution of *H. cyclobates*. He argues that its rounded shell and strong muscular grip are adaptations that would minimise predation, and that occupying seagrass areas would provide shelter from large visual predators. However, he also states that a larger body and shell size would provide better protection from predators, enabling the occupation of open substrata, whereas a smaller size would be better adapted for areas where food resources may be lower. Seagrass meadows may therefore be important to *H. cyclobates* for either or both of these reasons, but to date their relevance has not been clarified.

5.1 Predation & Food

5.1.1 Diet

Seagrass fragments comprised the majority of identifiable plant fragments in the stomach contents of *H. cyclobates*. A few animals had large quantities of a red alga which

frequently occurred as drift algae at Edithburgh. The remainder of the stomach contents consisted of unidentifiable organic material, which may be the remains of algae that were rapidly digested.

Foale and Day (1992) found that *H. rubra* could digest beyond recognition highly preferred algae in 6-12 hours. Many abalone, including *H. cyclobates*, begin feeding just after dusk (Shepherd, 1973; Mottet, 1978; Foale & Day, 1992), so although I collected abalone in the morning, food may have been present in their stomach for up to 14 hours, ample time for the digestion of preferred algae. Seagrass fragments did not appear to be easily digested and were readily detected in the rectum. Seagrasses are therefore unlikely to provide an adequate source of nutrition.

Seagrass blades, however, do support large numbers of epiphytic algae, including filamentous red algae. These epiphytic algae may be the source of the unidentifiable material, thus providing the bulk of the energy requirements for *H. cyclobates*. Shepherd (1973) found that epiphytes, together with their seagrass hosts, comprised the majority of the diet of *H. cyclobates* at Tipara Reef, South Australia. Seagrasses, by providing an abundant source of palatable algae, may therefore be indirectly important in the diet of *H. cyclobates*.

Abalone were found to have eaten similar amounts of food in both open and seagrass areas. Open areas may therefore not be as food-limiting as first thought. By browsing rock surfaces (Shepherd, 1973), *H. cyclobates* may ingest large quantities of small epilithic algae which would be quickly broken down, resulting in the large proportions of unidentifiable material found in the stomachs of animals from open areas. Alternatively, if open areas are food-poor, then foraging periods might be longer. Foraging periods of abalone are known to increase if food supplies are low (Poore, 1972; Mottet, 1978; Hines

& Pearse, 1982; Shepherd, 1986a). If *H. cyclobates* behaves similarly, then during the course of one night similar amounts of food may be ingested by abalone in open and seagrass areas, but this will not mean that foraging is equally efficient in the two habitats.

The power of these tests was insufficient to confidently detect significant differences. At the Northeast and Southeast sites the effect sizes (d) (Cohen, 1988) were either close to or less than the calculated effect sizes required to indicate a 20% difference in means. As the power to detect a 20% difference in means was low in each case, it is probable that the non-significant results obtained for these sites represent Type II errors. However, the direction in which the means differed between sites was interesting: more was eaten in seagrass areas at the Northeast and North site, whereas the pattern was reversed at the Southeast site and for the second sample collected at the North site (Table 3.1). This observation suggests that habitat type does not influence the amount of food eaten.

These results indicate that seagrasses are readily ingested by *H. cyclobates*, probably because they provide an abundant source of palatable epiphytic algae. However, abalone in open areas do not appear to be food-limited. Differences in the accessibility of food between the two habitats do not therefore adequately explain the observed distribution.

5.1.2 Predation

Predation is commonly cited as the main factor limiting species to vegetated areas (Heck & Orth, 1980; Stoner, A.W., 1982; Gotceitas & Colgan, 1989). In my study, there was no significant difference in short term survivorship of abalone between open and seagrass areas. Short term predation effects are therefore unlikely to explain the observed distribution. The effect of predation in the long term is unknown and different results may

have been obtained if a longer experiment using the method described by Beinssen & Powell (1979) to measure movement and natural mortality had been used. During the experiment, occasional instances of predation by the gastropods *Lyria mitraeformis* and *Pleuroploca australasia,* and the seastars, *Coscinasterias muricata* and *Uniophora granifera* were observed in both habtats. Most of these were observed shortly after the initiation of the experiment and may represent predation on animals stressed by handling. Some of the dead shells collected showed damage consistant with predation by crabs, possibly *Nectocarcinus integrifrons* a large predatory crab common at Edithburgh.

Few studies have found predation to be the principal determinant of abalone distributions (Hines & Pearse, 1982; Shepherd & Turner, 1985; Mower & Shepherd, 1988; Shepherd, 1990). Predators may influence the behaviour of abalone (e.g. nocturnal activity periods) so that the abalone minimise predatory encounters (Mottet, 1978), enabling a degree of co-existence. The presence of predators in both open and seagrass areas suggests that *H. cyclobates* have developed similar strategies.

5.1.3 Food Abundance

Haliotis cyclobates is less likely to move if an abundant food supply is easily available. Hunger is an important factor affecting the foraging behaviour of marine animals (McKillup & Butler, 1983; Olla & Davis, 1990; Johnsson, 1993), and many species of abalone alternate between passive and active foraging depending on the availability of food (Poore, 1972; Mottet, 1978; Hines & Pearse, 1982; Shepherd, 1986). Both strategies are efficient methods of obtaining food but passive foraging has advantages because it requires little energy and minimises the risk of predation (Shepherd, 1973; Hines &

Pearse, 1982). The presence of abundant food that can be obtained by passive foraging may therefore be a major factor explaining the higher density of *H. cyclobates* in seagrass meadows at Edithburgh.

Seagrass and open areas are patchily distributed at Edithburgh, so an actively foraging abalone, randomly moving across open areas, would eventually encounter a patch of seagrass. Provided suitable substrata occur in this habitat, active foraging is likely to cease. Therefore, migration from seagrass is likely to be less than movement into it; this process of orthokinesis (Fraenkel & Gunn, 1940) will result in higher abundances of *H. cyclobates* in seagrass than in open areas.

No positive shelter effects were detected. Seagrass is known to provide shelter for a range of species, but these are generally sediment dwellers (Summerson & Peterson, 1984; Irlandi & Peterson, 1991), epifauna (Edgar & Robertson, 1992) or fish which hide amongst the blades (Summerson & Peterson, 1984; Lubbers *et al.*, 1990; Sogard & Olla, 1993). For these species refuge is provided by the complex structure of the seagrass. Abalone occur on hard substrata to which they can firmly attach, thus resisting attack from predators. Seagrasses may afford *H. cyclobates* some protection from visual predators (Shepherd, 1973) but it is likely to be secondary to the importance of hard substrata.

If the presence of food that can be obtained by passive foraging is important in determining the local distribution of *H. cyclobates* then it may not necessarily be restricted to seagrass areas. The shallow-sand plot at the North site was found to have proportionally more abalone remaining in both the bare/shelter and food treatments than the other plots. During north-easterly storms the seafloor near this plot was frequently disturbed by wave action. Considerable quantities of drift-weed were noticed during these periods, often covering the seafloor in the experimental area. Therefore, abalone in the bare/shelter

treatments frequently had access to potential food. Their relatively limited dispersal in this plot is thus consistent with the hypothesis that food influences their movement. The presence of abundant food in the shallow plot also explains the greater number of abalone remaining in all treatments relative to the two deep plots. If this hypothesis is correct, then the presence of drift weed would also explain the high density of abalone naturally occurring at the North site.

The between plot comparisons found that the level of response to the presence or absence of food varied between all plots. The reasons for these differences are unclear but may be related to depth and the abundance of drift weed (discussed above) and/or the type of substratum present between the experimental patches within plots. The deep-rubble plot had numerous patches of hard substrata occurring between the experimental patches while the deep-sand plot only had sand. *Haliotis cyclobates* is potentially vulnerable to predators while on sand, so it may limit its movement across sand. This may explain why relatively fewer abalone moved away from the bare treatment in the deep-sand plot compared to the deep-rubble plot (see Table 3.9). The availability of patches of hard substrata may therefore be important in determining movement of *H. cyclobates*, which may influence its distribution, although it is likely to be secondary to the importance of food.

5.1.4 Conclusions

Although restricted to Edithburgh, these results indicate that the availability of abundant food is an important factor determining the distribution and abundance of *H. cyclobates*. Its occurrence in seagrasses elsewhere (Shepherd, 1973) and the importance of food in determining the distribution of other abalone (Shepherd & Cannon, 1988) suggest that

food is likely to be a major factor affecting the small scale distribution and abundance of *H. cyclobates* throughout its range.

5.2 Settlement & Recruitment

5.2.1 Spawning

Haliotis cyclobates has a single spring-summer spawning period at Edithburgh. The rapid decline of the gonad index in November 1993 suggests highly synchronised spawning within this population, which probably reflects at least one mass spawning event. This pattern is very similar to that observed by Shepherd and Laws (1974).

Calm weather is thought to be a major cue determining the onset of spawning for some abalone because it helps minimise the dispersal of eggs, sperm and larvae (Breen & Adkins, 1980; Prince *et al.*, 1987; McShane, 1992), although recent work suggests that some species spawn during storms, which presumaby increases the mixing and thus the fertilisation of gametes for non-aggregating species (Sasaki & Shepherd, 1995). In November 1993 two, three day stretches of calm weather occurred during the period in which spawning commenced. No periods of rough weather occurred in the same period. Interestingly, a set of spring tides also occurred in this period, coinciding with one of the calm periods. Fast currents during spring tides are considered to be possible spawning cues by Shepherd & Daume (1996), particularly for non-aggregating species.

Although only a correlation, it is not unreasonable to suspect that spawning commenced during one of the calm periods. Adults did not appear to aggregate for spawning (pers. obs.), and individuals were usually spaced 0.1-0.3m from their nearest neighbour, so fertilization depended on the successful union of gametes from non-adjacent individuals.

Gamete concentrations can be rapidly diluted over short distances (Pennington, 1985) and increased turbulence during rough weather may exacerbate this effect. Synchronised, mass spawnings during calm weather are therefore most likely to achieve the best rates of fertilization for *H. cyclobates*.

5.2.2 Settlement

New recruits (shell length less than 3mm) were predominantly collected from seagrass blades. Due to the small number collected firm conclusions about the settlement distribution can not be made, but their occurrence on seagrass is very interesting. Abalone apparently settle preferentially on crustose coralline algae growing on rocky reefs (Morse, D.E. *et al.*, 1979a, 1980; Morse, A.N.C. & Morse, 1984; Shepherd & Turner, 1985; Clavier & Richard, 1986; McShane & Smith, 1988; Moss & Tong, 1992b). Variable amounts of CCA do occur on seagrass (Steneck, 1986 and pers. obs.) which may explain the occurrence of newly settled juveniles.

If *H. cyclobates* settles preferentially on CCA then their absence from CCA encrusted rocks found in the study area is unusual. These substrata were available for settling larvae because new recruits of *Haliotis scalaris* were occasionally found on the patches of CCA. Possible explanations for the observed pattern are, 1) settlement was low throughout the area during the study period, 2) settlement occurs preferentially on CCA associated with seagrasses and 3) settlement occurs preferentially on seagrasses in response to an unknown cue.

Failure to detect newly settled juveniles and the absence of new recruits from the settlement substratum experiment apparently supports the hypothesis that settlement rates

were low during the 1992-1993 season. Seagrass, however, was not examined during this period, and if settlement occurs predominantly on it then the failure to detect settlement in the experiment is not surprising. Furthermore, numerous zero year class recruits were detected in 1993 indicating that reasonable levels of settlement must have occurred at some time. Similarly a reasonable number of zero year class recruits were found in 1994, suggesting that settlement failure was not the cause of the low number of newly settled juveniles found then.

It is impossible to tell from this study whether settlement on seagrass occurs in response to CCA or some other inducer. In the laboratory, abalone larvae will settle on non-CCA surfaces, particularly diatom/bacteria films (Hahn, 1989; Moss & Tong, 1992b; Slattery, 1992). Settlement has even been recorded on field placed artificial collecters with diatom and micro- algal films (Nash, *et al.,* 1995; Keesing, *et al.* 1995) . On rocky reefs CCA is abundant and therefore a suitable settlement substratum for reef dwelling species. Its patchy distribution on seagrass would reduce its suitability as a settlement inducer, so *H. cyclobates* may have settlement behaviour adapted to include either CCA or other suitable organic surfaces. Settlement on either CCA or organic films has been observed in the gastropod *Trochus niloticus*, which may help to increase the number of potential settlement sites (Heslinga, 1981). Similar behaviour by *H. cyclobates* would increase the chance of successful settlement within a seagrass meadow.

Even if settlement is restricted to patches of CCA, it is unlikely that CCA plays any further role in providing habitat and food for the newly settled juveniles of *H. cyclobates*. Juveniles of reef dwelling species inhabit CCA for the first 6 to 12 months, browsing the surface and ingesting CCA fragments which turn their shell pink, thus camouflaging the juveniles while they remain on the CCA (Crofts, 1938; Shepherd, 1973; Garland *et al.*,

1985). Juvenile *H. cyclobates*, including newly settled juveniles, are not found on CCA and they do not have pink shells (see PLATE 4.1), suggesting that CCA may not be important for their early development and survival. This aspect requires further investigation as shell colour is not always a reliable measure of settlement substratum.

5.2.3 Recruitment

New recruits were found on patches of hard substrata between March and October, with peak abundance occurring in April. This pattern supports the single spawning and settlement period discussed earlier, and enables the identification of separate cohorts. Recruits were found in all habitats in March 1994. The number of recruits found varied between sites and habitats but, except for the southern site, too few juveniles were found to identify specific site or habitat differences. The results suggest either wider settlement than previously discussed or that post-settlement migration has occurred from seagrass to open areas. Although widespread settlement can not be rejected, it is plausible that post-settlement migration occurs following settlement predominantly on seagrass blades. Zero year class *H. cyclobates* are capable of moving at least two metres in one night (pers. obs.).

The ambiguity of these results arises because the size-frequency surveys could not be continued beyond mid-March 1994. According to the 1993 data for the South seagrass site, peak recruitment did not occur until the end of April. Continuing the 1994 surveys up to May might have detected stronger recruitment, enabling site and habitat comparisons to be made.

Based on the distribution of newly settled juveniles, recruitment onto hard substrata in seagrass meadows would appear to be adaptive behaviour. As the juvenile grows it would become more visible to predators while it remained on seagrass. Migrating to cryptic sites on hard substrata would help minimise the risk of predation, while remaining in the seagrass meadow would ensure that an abundant food supply was nearby. Juveniles of other abalone species all behave similarly, migrating to cryptic habitats when they attain larger sizes (Shepherd, 1973).

5.2.4 Conclusions

These results suggest that the spawning, settlement and recruitment behaviour of *H. cyclobates* is adapted for living in seagrass areas. It is unclear from these results whether preferential settlement and recruitment into seagrass areas occurs, or if post-settlement processes have altered initial settlement patterns. To properly understand the importance of seagrass a comprehensive survey of settlement and recruitment patterns must be done. However, if seagrass areas enhance recruitment compared to open areas then this may establish patterns that result in the observed distribution of adults.

5.3 Conclusion

Aspects of the early life history of *H. cyclobates* and the presence of abundant food both explain its predominant occurrence in seagrass areas. The relative importance of each is, however, difficult to determine. The occurrence of high densities of abalone in food-rich areas suggests that food is an important determinant, particularly for the adult population.

However, the early life history of *H. cyclobates* appears to enhance recruitment into seagrass areas. The two processes probably complement each other. Preferential settlement and recruitment into seagrass meadows ensures an abundant food supply for young juveniles and minimises the risk associated with migrating between juvenile and adult habitats (O'Connor, 1993). Older juveniles and adults may distribute themselves according to the location of abundant food sources. In most instances this would result in the abalone remaining in seagrass areas, although the occupation of open areas may occur if food is abundant and easily obtainable.

Predation was not found to affect the distribution and abundance of *H. cyclobates*. Long term predation pressures may have some effect, but it is likely to be weak given the avoidance strategies utilised by *H. cyclobates*. Furthermore, any effect is likely to be masked by the rapid response to the presence or absence of food.

Previous work on *H. cyclobates* has only investigated its basic distribution and biology. This study has advanced this basic knowledge by identifying the factors important in determining its local distribution. Some of the results, such as the role of drift weed and the long term movement of adults and juveniles in determining local distributions, and the spawning behaviour of adults warrant further investigation, preferably at different locations. Of particular interest is its settlement distribution and substratum, clarification of which would contribute to the current debate about the settlement behaviour of abalone.

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