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STUDIES ON THE RECRUITMENT  
AND  
STOCK DENSITY OF THE GREENLIP  
ABALONE (Haliotis laevigata)

FINAL REPORT

PART I

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## \*NT ODUCTION

The purpose of the grant was to examine the recruitment of greenlip abalone, in relation to various biotic and abiotic factors. Those considered important included:

- 1) factors affecting egg production (fecundity) and fertilisation success (aggregative behaviour);
- 2) factors affecting settlement strength - e.g. size of parent stock (assuming a parent-progeny relationship existed); oceanographic features affecting the numbers of larvae transported to the site of larval settlement; substrate characteristics affecting larval behaviour;
- 3) factors affecting survival of newly settled abalone.

All three questions were addressed. The strategy adopted was to:-

- (a) examine recruitment and stock size relations, effects of oceanographic conditions, habitat preferences of newly-settled abalone, and the aggregation behaviour of spawning adults at West I. This site was chosen for ease of accessibility and the fact that 10 years data on recruitment and stock had accumulated (although then unanalysed). A field laboratory was built on the island and this complemented the intensive underwater studies that were conducted there.
- (b) examine inter-annual and spatial differences in recruitment strength at Waterloo Bay. This Bay lent itself to such a study by reason of its varied bottom topography and the fact that it had been well studied by the author and there was an accumulated corpus of knowledge already on recruitment and stock size of abalone there. The Bay contained what was believed to be an isolated stock so that a parent-progeny relationship should, if it existed, be discernible. This was aided by the circumstance that fishable stocks collapsed in about 1981, and the Bay was closed to fishing in April 1982. The Bay is due for re-opening in April 1986. Measurement of recruitment during this period, with changing stock size, will provide data on the parent-progeny relation, and also enable an assessment of the value of closures. The study is still current, and is planned to terminate in 1986.
- (c) recruitment and stock size were measured at a number of other sites as part of a general monitoring program. The sites were Cape Jervis (6 sites), Tiparra Reef (5 sites) and Investigator Group of islands (16 sites).

A methodological problem here was to devise a way of estimating density of recruits and adults. The problem has been only partially solved and will be described in detail in Part 2 of the report.

In all a very extensive research program was undertaken, and this accounts in part for the delay in presenting this and subsequent reports. This report will consider only items in (a) above. Results of studies in (b) and (c) will be presented subsequently.

The data in (b) and (c) were part of longer term programs that began before and continued after the currency of the grant. Analysis of these data will be undertaken when the respective studies are complete.

## RESULTS

A brief commentary on the results is given below. Manuscripts containing data and their analysis are attached as appendices.

### 1. Factors affecting egg production and fertilisation

#### Fecundity

The fecundity (maximum number of eggs produced) of greenlip was examined for a number of populations (Appendix 1).

A major finding was the apparent inverse relation between "environmental favourableness" (as measured by the anabolic growth parameter K. Loo) and relative fecundity. Subsequent work has shown that the situation is even more complex. Within population differences in relative fecundity according to environmental favourableness show the opposite trend to inter-population differences. The matter is now being examined by field experiments involving cross-transplants between sites with differing characteristics of environmental favourableness.

#### Aggregation behaviour

An understanding of the aggregative behaviour of abalone is important because it increases the harvesting efficiency of divers who search for abalone clumps, rather than individuals. This increases the risk of recruitment overfishing.

The results of the study (Appendix 2) show that aggregative behaviour is tied to sexual maturity and the spawning season. Aggregative behaviour develops after attainment of sexual maturity and strengthens with age. It is not yet known whether the contribution of sexually mature 3 and 4 year olds to the pool of abalone larvae is relatively less than that of older age classes because of the lower aggregative tendency. This may be of some practical importance in interpreting the results of recruitment-spawning stock relations for West I (Appendix 6).

### 2. Factors affecting settlement strength

Two significant developments in techniques allowed the completion of a satisfactory program at West I.:

- (a) the design and construction of an underwater magnifier enabling recognition of juveniles < 1mm long, and

- (b) the development of an experimental habitat which offered a simple, replicable, and uniform technique for measuring settlement strength of abalone in situ.

The results of the study are given in Appendix 3. Because settlement of 2 species of abalone occurred it became necessary to sort out spawning and settlement of a second species (Haliotis scalaris). Information on this species is given in Appendix 4.

To assure the success of the experimental habitats maintenance of a healthy crustose coralline layer for abalone to settle on was critical. Experimental manipulations with archaeogastropod grazers showed that these species by grazing off filamentous algae as they grew, indirectly maintained the crustose corallines. Thus the success of experimental habitats depend on maintaining on them a suite of grazing archaeogastropods and chitons. The results of a study of archaeogastropod grazing are given in Appendix 5 (this includes data external to the grant).

Overall, these findings have enabled the routine measurement of settlement strength of abalone, and determination of the timing of settlement. This is highly significant because it will lead to (a) determining the set of oceanographic conditions most favourable to settlement and (b) allow measurement of pre-recruit mortality.

3. Factors affecting survival of newly-settled abalone

Wrasses were found to be important predators of small abalone 10-50mm size. Because wrasses are nearly ubiquitous in most places studied, some information was obtained during (and after termination of) the grant on the feeding and behavioural aspects of the blue-throated wrasse. Preliminary findings are given in Appendix 6.

4. A major work has been to review population size, mortality and recruitment of abalone at West I. over 14 years (Appendix 7).

A major result was the recruitment - sea temperature relationship. This opens up many new areas of investigation.

Other findings of interest include the density dependent mortality and recognition of the importance of stingrays as predators of adults. It must be borne in mind that West I. has an unexploited population of abalone, so that fluctuations in mortality rates are much more likely to occur there (due to predator behaviour) than at exploited sites where abalone densities would change much less.

## CONCLUSIONS

The grant enabled considerable progress to be made toward an understanding of the numerous processes affecting recruitment.

The most significant findings were:

- the relation between recruitment and sea temperature
- habitat preferences of newly settled abalone
- development of experimental habitats to monitor settlement of abalone
- assessment of important predators at different sizes.

Problems which need to be addressed are:-

- validation of the sea temperature - recruitment hypothesis for the principal areas of the fishery
- the parent-progeny relationship
- mortality (and its agents) of abalone 1-10mm long.

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2. The aggregative behaviour of H. laevigata.
3. Habitat preference, abundance and predators of juveniles.
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5. Distribution and feeding of archaeogastropods in a boulder habitat at West I., South Australia.
6. Extract of paper on feeding of the blue-throated wrasse, and abalone size preferences by different size classes of wrasse.
7. Recruitment and mortality of H. laevigata over 14 years with notes on predators of adults.

APPENDIX 1

Fecundity and sex ratio of H. laevigata at different sites (ms).

STUDIES ON SOUTHERN AUSTRALIAN ABALONE (GENUS HALIOTIS)

VIII. FECUNDITY AND SEX RATIO OF H. LAEVIGATA AT DIFFERENT SITES

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SUMMARY

Fecundity and sex ratios of Haliotis laevigata Donovan were examined at a number of sites in South Australia. At all sites fecundity has a linear dependence on weight. There is an inverse correlation between relative fecundity and environmental favourableness, i.e. sites with high growth rates tend to have lower fecundity.

Sex ratios show a linear dependence on size at most sites. At four sites the proportion of females increases with increasing size, at two other sites there is the opposite trend and at one site the sex ratio is equal.

The significance of different fecundities and changing sex ratios is discussed.



## INTRODUCTION

The fecundity of a species is an important life history trait that has co-evolved with other life history traits to provide the optimal tactic for a species in a given situation. Energy available as food to an individual must be shared between the competing demands of reproduction, growth and maintenance. The interactions and trade-offs that occur between these demands are reviewed by Stearns (1976) who described models that predict under what conditions reproductive effort (fecundity) is less than the maximum possible.

This paper describes the fecundity and sex ratio of an abalone species at different sites and considers the significance of the differences found.

The abalone Haliotis laevigata Donovan is a K-selected species (Stearns 1976) which shows iteroparity, has a delayed first reproduction, a relatively long life and low mortality. It produces a large number of eggs hatching into lecithotrophic larvae which are planktonic for a few days before settling in suitable habitat (Shepherd and Turner 1985).

The sites selected for the study of fecundity (Fig. 1) are principally those where recruitment, growth and mortality are being or have been examined. Other sites have been added where data became available.

## MATERIALS AND METHODS

H. laevigata spawns from October to March (Shepherd and Laws 1974). Samples were collected for analysis in 1981 or 1982 during August or September, prior to the commencement of spawning when ova are large and rounded. The number and size range of individuals examined, and sample

locations are given in Table 1. Shell length and total weight (TW) were recorded for each female and the ovary and visceral mass excised and preserved in 10% formalin and sea water until firm.

After separation from the viscera, the ovary was weighed: subsamples of 1-4 mg from its anterior, middle and posterior parts were taken and weighed to the nearest 0.1 mg and the number of ova in each subsample counted under a low power binocular microscope. The mean egg weight was calculated and by simple proportion, the number of eggs per individual estimated.

The relationship between fecundity (number of eggs produced) and weight were obtained by least squares linear regression analysis.

Population sex ratios were determined from samples collected by research staff or from examination of catches of commercial divers, during August or September when individuals can be sexed visually (Shepherd and Laws 1974). For each sample sex ratios were obtained for successive 20 (in one case 30) mm size classes and Cochran's (1954) test used to test for a significant change in sex ratio with length.

## RESULTS

### Fecundity

The equations relating fecundity (E) and total weight of H. laevigata for six sites are given in Table 1 and shown graphically in Fig. 2. In each case fecundity increases linearly with weight (and hence with a power of length). The slopes of the fecundity curves differ significantly between sites. The relation between fecundity and 'favourableness of the environment' was examined by searching for a correlation between the

slope of the regression of fecundity on weight and the anabolic growth parameter  $K_{Loo}$  where  $K$  and  $Loo$  are the growth parameters of the Von Bertalanffy growth curve.

The slope of the regression can be considered a measure of relative fecundity defined as the number of eggs produced per unit weight (Bagenal 1973). Shepherd and Hearn (1983) found that the parameter  $K_{Loo}$  was correlated with the food supply for 3 sites, and hence may be considered as a crude index of environmental favourableness (vis-a-vis abalone) which is very difficult to estimate directly. Estimates of the growth parameters,  $K$  and  $Loo$  are given in Table 2. There is a significant inverse correlation by the simple test ( $r = -0.85$ ;  $p < 0.05$ ) and by Spearman rank ( $r_s = -0.91$ ;  $p < 0.05$ ) after ranking of the variables.

#### Sex ratio

Samples taken at 7 sites were subjected to a  $\chi^2$  test (Cochran 1954) to detect a linear dependence of the sex ratio on size. The results are given in Table 3. At four sites (West Island, Tiparra Reef, Waterloo Bay and Sheringa) the proportion of females increases with increasing size, at two sites (Ward I and Flinders I) there is a reverse trend, and at the Hotspot there is no significant change.

### DISCUSSION

#### Fecundity

The relationship between fecundity and weight is linear and similar to those given for other species of Haliotis (Newman 1967, Poore 1973). However, Sainsbury (1982) found a polynomial relationship in which

fecundity decreased in the largest size class.

The differences in slopes of the fecundity curves between sites demonstrate that these populations have evolved different life history strategies in different environments. The correlation of relative fecundity with environmental favourableness (as perceived by this abalone) suggest the allocation of relatively more energy into growth in favourable than in unfavourable conditions. However life history data (including information on larval survival) for the various sites are far too scanty to be confident that this is the true explanation. All we can be certain of is that factors are operating which cause some populations to evolve with a smaller than maximum reproductive effort.

Environmental favourableness may itself have equivocal effects and there are both examples where increasingly harsh environments have increased energetic investment in reproduction (Dearn 1977, McKillup and Butler 1979) and decreased such investment (Bagenel 1973).

#### Sex ratios

While unequal sex ratios have been observed in a few abalone species (Sinclair 1963, Forster 1967, Giorgi and Demartini 1977, Quintanella and Aceves 1976) and equal sex ratios in others (Crofts 1929, Boolootian et al. 1962), Newman 1967, Young and Demartini 1970), there have been no studies of changes in the sex ratio with size or between populations except earlier notes by Shepherd and Laws (1974) and Shepherd and Hearn (1983), and the study of Tutschulte and Connell (1981).

The significance of a changing sex ratio with size is still not clear. Shepherd and Hearn (1983) found that female H. laevigata

grew 25% faster than males at Waterloo Bay and suggested that this differential growth was the most likely reason for the changing sex ratio there. Differential mortality between the sexes is possible but seems improbable because there are no external physical or known behavioural differences between the sexes. Surplus energy available after body maintenance needs have been met may be used in growth and/or reproduction. The allocation of relatively more energy to one will reduce the energy available to the other (Levins 1968). Different populations could well evolve slightly different strategies for the allocation of energy if, for example, there is a greater relative advantage at a given site to grow as fast as possible in order to produce more eggs later in life (e.g. Creese 1980). A result of these differences may be different sex ratios at different sites. This suggestion assumes that sex ratios and 'allocation strategies' are heritable traits and therefore capable of being naturally selected.

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TABLE 1

Values of the regression parameters of the equation relating fecundity (E) in millions of eggs of *H. laevigata* to total weight (W) in g. The equation has the form  $E = aW + b$ . N. = number; R<sup>2</sup> = correlation coefficient

	X-intercept			N	R <sup>2</sup>
	a	b	(g)		
West Island	0.0151	-0.381	25.3	36	0.82
Tiparra Reef	0.0246	-0.971	87	35	0.64
Waterloo Bay	0.0040	-0.363	72.8	32	0.34
Hotspot	0.0143	-4.281	299.4	25	0.59
Ward I	0.0080	-1.866	233.3	27	0.51
Pearson I	0.0113	-2.506	221.8	29	0.56

TABLE 2

Estimates of the parameters of the Von Bertalanffy growth curve for various sites with authority.

Site	K	Loo	K. Loo	Authority
West Island	0.48	138	66.2	Shepherd and Hearn (1983)
Tiparra Reef	0.41	131	53.7	Shepherd and Hearn (1983)
Waterloo Bay	0.59	148	87.3	Shepherd and Hearn (1983)
Hotspot	0.6	145	87.0	Analysis of length frequency data (unpublished)
Ward I	0.6	161	96.6	Analysis of length frequency data (unpublished)
Pearson I	0.6	145	87.0	Analysis of length frequency data (unpublished)

TABLE 3

Change in sex ratios at seven sites. The change in sex ratio is shown by comparing that of the smallest and largest size classes respectively.

Site	Number Examined	Size range (mm)	Change in Female to Male Sex Ratio	$\chi^2$	P
West Island	332	85-157	0.36 - 1.24	5.00	<0.03
Tiparra Reef (South B)	198	78-135	0.65 - 2.25	13.30	<0.000
Tiparra Reef (West B)	234	77-156	0.46 - 1.88	7.69	<0.01
Waterloo Bay	923	130-190	0.82 - 1.38	6.90	<0.01
Sheringa	200	130-188	0.71 - 1.00	12.02	<0.001
Hotspot	174	137-196	0.85 - 0.73	0.49	n.s
Ward I	312	127-206	1.45 - 0.94	5.00	<0.03
Flinders I (south east side)	202	127-186	1.85 - 0.38	30.21	<0.001

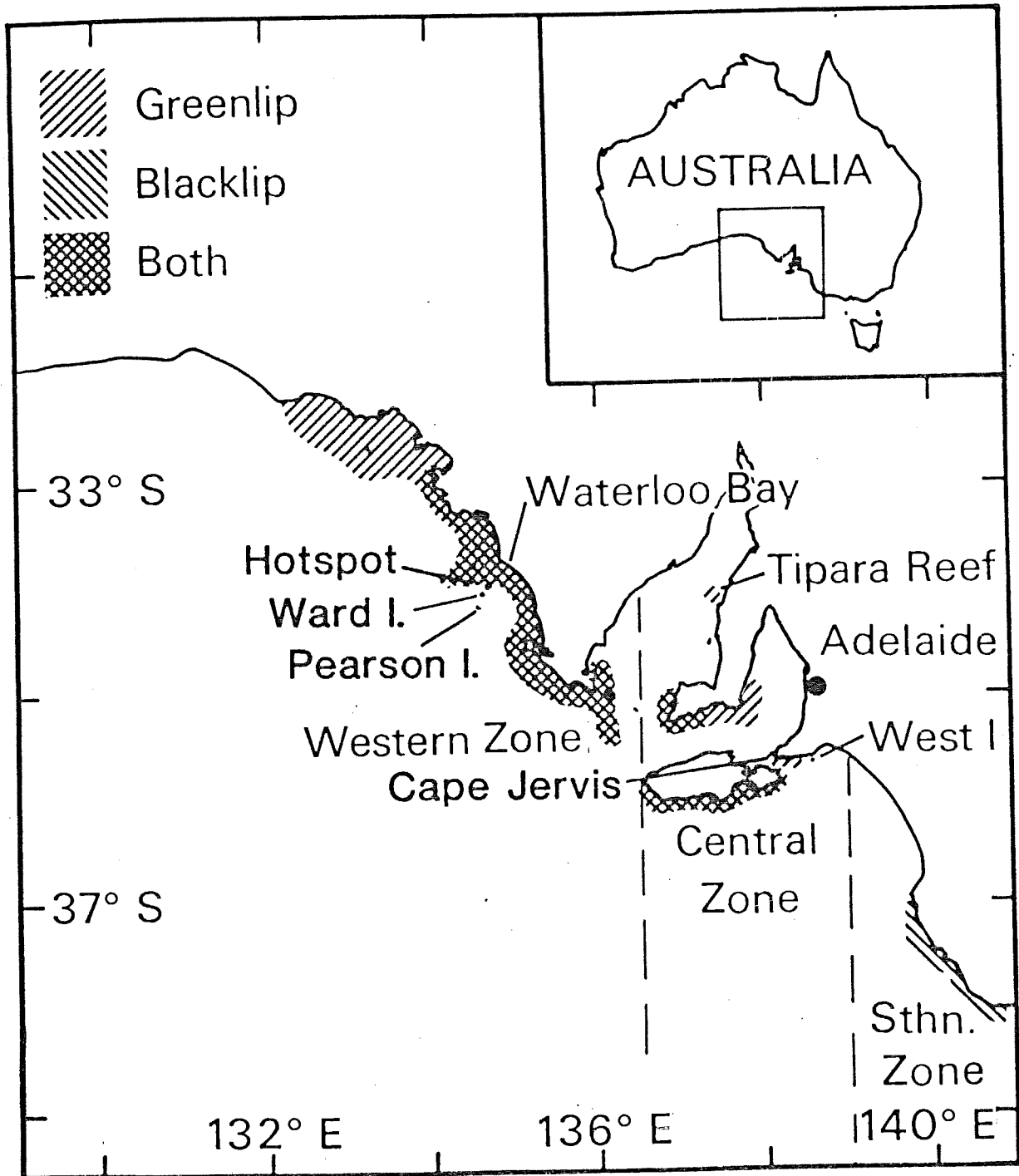


Fig. 1 Map showing sites referred to in the text.

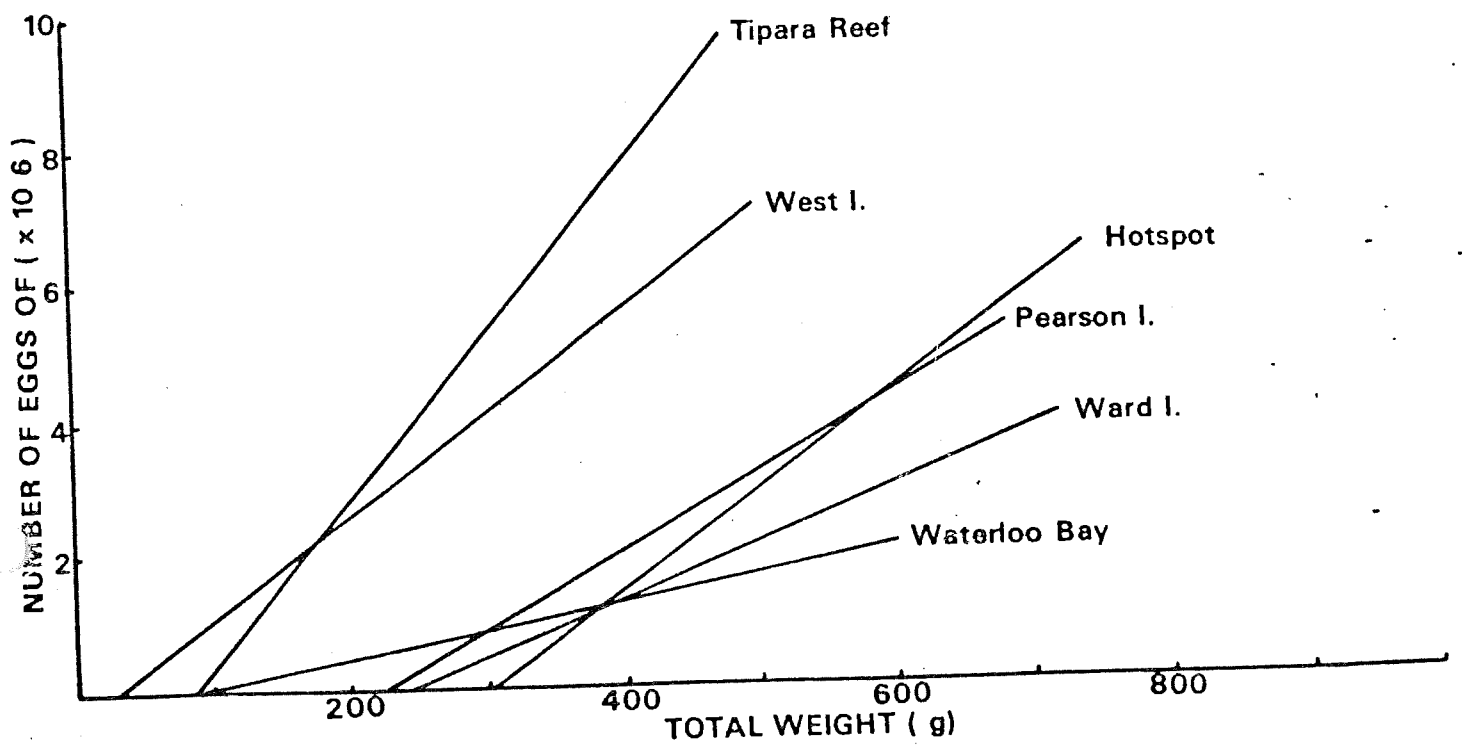


Fig. 2 Linear regressions between number of eggs ( $\times 10^6$ ) and total weight (g) for *H. laevigata* at various sites.

APPENDIX 2

The aggregative behaviour of H. laevigata.  
(ms submitted to Mar. Biol.).

STUDIES ON SOUTHERN AUSTRALIAN ABALONE (genus Haliotis)

VII. The aggregative behaviour of H. laevigata

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ABSTRACT

The aggregative behaviour of the abalone Haliotis laevigata was examined in the field at West Island and experimentally at Waterloo Bay, South Australia. Sexually mature individuals display aggregative behaviour just before and during the spawning season but tend to be randomly distributed at other times of the year. Sexually immature individuals show no such behaviour and are regularly to randomly dispersed. The tendency to aggregate increases with increasing age on attainment of sexual maturity. Experimental manipulations of adults only temporarily interrupts the dispersion pattern at a given time. The implications of the behaviour in managing exploited stocks are discussed.

INTRODUCTION

Abalone, like most other archaeogastropods, release their eggs directly into the surrounding seawater, where fertilisation occurs (Fretter and Graham 1962, Webber 1977). Behavioural mechanisms which bring male and female together could, therefore, be expected to have evolved to facilitate synchrony of release of gametes, and increase the successful fertilisation of spawned eggs. Such mechanisms that have been described include pairing of individuals and the formation of aggregations (Webber 1977).

It is well established that abalone tend to occur in aggregations (e.g. Newman 1966, Shepherd 1973), but it is not clear whether these are

for spawning or are simply concentrations of animals at favoured sites. The only study which has unequivocally related aggregation and spawning is that of Breen and Adkins (1980) describing spawning by Haliotis Kamschatkana Jonas.

If spawning, or its approach, induces aggregative behaviour, then this tendency might be expected to be more pronounced during the spawning season and after attaining sexual maturity. This study set out to determine the pattern of dispersion of adult Haliotis laevigata Donovan, and changes in that pattern both seasonally and between length classes.

The commercially exploited abalone H. laevigata occurs on rocky bottom and is often associated with crevices (Shepherd 1973). Populations at West Island (35°36'25"S, 138°35'27"E) and Waterloo Bay (33°39'S, 134°54'E) South Australia, have been studied for some years (Shepherd et al. 1982, Shepherd and Hearn 1983) and were used in this study. West Island is permanently closed to fishing, and Waterloo Bay was temporarily closed during this study.

H. laevigata is sexually mature in the 3rd year at a length of about 100 mm, at West I. and 120 mm at Waterloo Bay, but significant egg production does not occur until the 5th or 6th year (Shepherd in prep.). The spawning season is from October to March (Shepherd and Laws 1974).

The pattern of dispersion of H. laevigata at West Island from November 1981 to November 1983 is described, as well as the results of experimental manipulations of the dispersion pattern of H. laevigata at Waterloo Bay at the beginning and end of the spawning season.

## MATERIALS AND METHODS

### West Island

H. laevigata occurs at the base of a boulder slope where rock meets the sand in Abalone Cove (Shepherd 1973) among boulders mostly 30-40 cm long by 20-30 cm wide; this is the site where all previous studies have been made (Shepherd et al. 1982; Shepherd and Hearn 1983). The area studied extended 55 m along the base of the slope over a band width of 1 m. A 50 m tape and the sandline marked the upper and lower boundaries of the band, and permanent marks were set at each end. Adult abalone densities were 3-4 m<sup>-2</sup> for about one half of the area and about 1 m<sup>-2</sup> for the other half. At about 3 monthly intervals (more frequently in spring) a diver counted all abalone that he could find in a 1 m<sup>2</sup> quadrat placed contiguously and sequentially through the area. Numbers of abalone were recorded in three length classes, viz. 100-110 mm, 111-120 mm and > 120 mm; small abalone < 100 mm long are not all sexually mature (Shepherd and Laws 1974) and were excluded.

From the growth curve of H. laevigata at West Island (Shepherd and Hearn 1983) with knife-edge separation between age-classes, the length range at age 3 is 90-109 mm and at age 4 is 110-119 mm. Thus the length classes examined correspond crudely with the 3, 4 and > 5 year old individuals. The correspondence between length and age is more satisfactory for the 3 year age class than for older ones which are increasingly confounded due to the decreasing annual growth increment with increasing age.

In addition, at the same site the diver measured the nearest neighbour distances between all individuals that he could find > 100 mm long; these were recorded for the same three length classes i.e. 100-110 mm,



110-120 mm and > 120 mm. Measurement of distances between individuals within, and nearest neighbours outside, the area were included to avoid bias due to the edge effect.

#### Waterloo Bay

On 27 October 1983 a 2 m grid of weighted polypropylene rope was laid down in an area 10 m x 10 m on calcrete limestone in the centre of Waterloo Bay at about 9 m depth. Low ridges or peaks, of about 15 cm relief, colonised by algae of the Cystophora - Sargassum - Osmundaria community (Shepherd and Womersley 1981) were scattered through the area and H. laevigata occurred in shallow troughs between the ridges. The position of all H. laevigata initially in the area at the start of the experiment was measured by reference to the grid and marked on a map, and all individuals (except those < 100 mm long) were removed.

Individuals > 120 mm, some taken from outside the area, were marked by a groove in the shell and placed on the bottom in a regular array at each intersection of a 1 m grid superimposed on the original grid, except that none were placed within 2 m of the perimeter. Thus 49 individuals, each 1 m apart were uniformly distributed over a 6 x 6 m grid. A nearby area of 8 m<sup>2</sup> served as a control. After 3 days the location of all abalone in the 10 x 10 m area and the control site was recorded as X and Y co-ordinates on each 2 x 2 m grid.

The experiment was repeated at exactly the same location and in the same manner on 27 April 1984. Abalone were removed and replaced in a regular array and the site re-examined and the location of abalone determined 3 days later.

### Statistical Analysis

The samples at both sites were taken to be fully censused populations rather than samples of larger populations. Conclusions are therefore strictly applicable only to the experimental areas, but the results should apply equally well to other similar areas occupied by the species.

The quadrat data from West I. were analysed in 3 cumulative length classes (i.e.  $\geq 100$  mm,  $\geq 110$  mm and  $\geq 120$  mm). The variance to mean (v:m) ratio applied to numbers in the 3 length classes in each quadrat (Greig-Smith 1957) was used as an index of dispersion to measure the dispersion pattern. At the scale selected (1 m<sup>2</sup>) the value 1 indicates a random pattern, and larger values clumping or aggregation. The significance of aggregation was tested by a t test and a X<sup>2</sup> goodness of fit test. Cumulative length classes were examined because the dispersion pattern of the two smaller length classes (100-110 mm, 110-120 mm) independent of larger length classes has little biological interest.

Nearest neighbour measurements were analysed by using the dispersal coefficient (R) of Clark and Evans (1954), calculated as follows:

$$R = \frac{\sum r}{N} \times 2 \sqrt{d}$$

where r = distance between each animal and its nearest neighbour, N = number of animals and d = density of the animal in the area. Mean density values were obtained from the quadrat data.

An R value of 0 corresponds to complete aggregation, 1.0 to a random distribution and 2.15 to regular dispersion. The statistic has biological meaning because, in any distribution, the mean observed distance to nearest neighbour is R times as great as expected in a random

distribution. Thus, an R value of 0.5 indicates that nearest neighbours are, on average, half as far apart as expected under conditions of randomness (Clark and Evans 1954). Simberloff's (1979) modification to the formula, allowing for the diameter of the animal, is unnecessary because the diameter of this abalone (10-15 cm) is less than half the expected mean nearest neighbour distance between points. The value of R was calculated separately for the three length classes 100-110 mm, 110-120 mm and  $\geq 120$  mm, and the significance of the values tested by the formula given by Clark and Evans (1954).

#### Waterloo Bay

The v:m ratio was calculated on 1 m<sup>2</sup> quadrat data for (a) the whole population recorded in the 100 m<sup>2</sup> area, and (b) the subset  $\geq 120$  mm long. The R statistic was obtained for those (a)  $\geq 120$  mm long and (b)  $< 100$  mm long (those 100-120 mm long having been removed). These length classes were selected for comparison because 100 mm is about the length when individuals first become sexually mature, and 120 mm when all are sexually mature (Shepherd and Laws 1974).

### RESULTS

#### West Island

Changes in the two statistics from 1981-4 are shown in Fig. 1. In most months sampled the v:m ratio for the largest length class ( $\geq 120$  mm) showed a significant departure from randomness toward aggregation. Values were generally higher from October to December than at other times of the year. The incorporation of smaller length classes sharply increased the v:m ratio from October to December, but had a variable effect at other times. Except for three samples (see below), the v:m

ratio for the 3 cumulative length classes from November 1981 to March 1984 (Fig. 1) all showed significant aggregation. Values of the t test used for significance ranged from 2.0 to 18.3 with sample sizes of 48-58 quadrats. Of the three samples which did not show significant aggregation (24 May 1982 for those  $\geq 110$  mm,  $t = 1.44$  n.s.; 29 March 1983 for those  $\geq 120$  mm,  $t = 1.6$  n.s. and 2 March 1984 for those  $\geq 120$  mm  $t = 1.6$  n.s.), the second was significant according to the  $\chi^2$  test ( $\chi^2 = 6.02$ ;  $P < 0.05$ ). The R statistic measures the pattern of dispersion of each length class. The largest ( $\geq 120$  mm) length class is significantly aggregated from October to February each year (in each case  $P < 0.01$  except January 1983 when  $P < 0.05$ ) and at other times randomly dispersed (Fig. 1). The intermediate (110-120 mm) length class is significantly aggregated ( $P < 0.05$ ) for some but not all sampling dates in the period October-February, and the smallest length class is mostly randomly, but sometimes regularly (e.g. October 1982;  $P < 0.001$ ) dispersed.

The results are more readily interpreted by conversion of the length classes to approximate age (see Methods), notwithstanding the partial confounding of older (4 and 5 year) age classes that occurs, and then plotting the change in the R statistic with increasing age (Fig. 2). It is apparent that the dispersion pattern shifts gradually from a regular or random one prior to age 3 to an aggregated one during the spawning season at ages 4 and 5. Between spawning seasons the pattern reverts to a random one.

#### Waterloo Bay

Changes in the v:m ratio and the R statistic before the October experiment, immediately after the manipulation of location and density of large

(> 120 mm) abalone and at the end of the experiment, are given in Table 1.

At the commencement of the experiment, large abalone were aggregated and small abalone were randomly distributed in the area. The manipulation resulted in a regular distribution pattern of all abalone throughout the area. After 3 days the position of only 5 abalone remained unchanged and large abalone were significantly aggregated, but small ones remained randomly dispersed as shown by changes in the R statistic (Table 1).

The v:m ratio showed the same changes in dispersion of the largest length class (> 120 mm), although the whole population shifted from a random to an aggregated pattern of dispersion. Because the experimental clearing of large abalone from the perimeter of the area and the edge effect may have biased the two statistics, they were recalculated after excluding data from all 1 m<sup>2</sup> quadrats around the perimeter of the area. The differences (Table 1) were trivial. There were slight changes in the statistics for the control, probably due to the relatively small sample size, but no strong trend is evident.

The April experiment gave very different results. Immediately prior to the experimental manipulation abalone were randomly distributed (except in the control where numbers of small ones caused a temporary aggregation pattern in the sample). After 3 days the position of only 5 abalone remained unchanged, and the distribution was random in the plot and the control.

#### DISCUSSION

The two statistics used to describe the dispersion pattern show the same trends although they do not always agree in detail. Where they disagree

the R statistic is probably the more reliable partly because it is based on distance measurements and partly because the v:m ratio is known to be sensitive to quadrat size and density (Greig-Smith 1957).

Although widely reported by commercial abalone divers, aggregative behaviour has only occasionally been noted in studies of abalone (Poore 1972, Newman 1966, and only once examined (Uno et al. 1972). The latter authors found that the intensity of aggregation of Haliotis sieboldii decreased after the spawning season.

A number of mechanisms have been proposed to explain aggregation in molluscs. They are (a) habitat heterogeneity and (b) various facilitation behaviours by which individuals benefit in some way by the closeness of conspecifics. Examples of these behaviours are: a group defence mechanism, food sharing and spawning. These are each considered in relation to abalone.

If the habitat is heterogeneous, a species will tend to occur in a restricted number of favourable sites and may then show an aggregated distribution pattern. This is better known for intertidal than subtidal molluscs (Underwood 1976 a,b). In this study the two sites were selected because, at the scale examined, they were relatively uniform, i.e. there were no apparent habitat differences which could account for any observed dispersion pattern. Hence habitat heterogeneity can be excluded as a factor at these sites.

Of the 3 facilitation mechanisms, food-sharing is unlikely because drift algae on which this species feeds is in superabundance (Shepherd 1973, Shepherd and Hearn 1983), and individuals have very rarely been observed

sharing the same piece of drift alga. This contrasts with the study of Duggins (1981) who recorded a high incidence of sharing of drift algae between three species of sea-urchins.

Aggregation is well established as a group defence mechanism for species such as sea-urchins whose spines can form a formidable array to a predator (Pearse and Arch 1969, Bernstein et al. 1983). However, it is a tactic of doubtful utility for adult abalone, whose major predator is the sting-ray (Shepherd 1985). The evidence is, rather the other way, namely that aggregation may be a disadvantage because predators are more successful when searching for clumped, than for randomly dispersed, prey (Tinbergen et al. 1967, Croze 1970, Taylor 1977).

Aggregation is thus most plausibly associated with spawning. The clumping pattern, for example, becomes established only with increasing size after attainment of sexual maturity, is strongest during the spawning season, and relaxes between spawning seasons. Field manipulations only temporarily interrupt the pattern in the spawning season and demonstrate that it is not a merely passive response to environmental factors.

Because the species lives in places of vigorous water movement (Shepherd 1973) and fertilisation of gametes is external, aggregation seems essential to synchronise release of male and female gametes and so secure successful fertilisation.

The aggregative behaviour of abalone may have practical significance in managing fish stocks. Fishing mortality rates are likely to be higher for aggregated abalone than more randomly dispersed ones (Breen and Adkins 1980), and this may have a strong effect in excessively reducing the

adult stock and thus affecting recruitment.

Recruitment overfishing is a problem which has afflicted many abalone stocks (Wyner et al. 1977; Doi et al. 1977; Breen 1985), and Sluczanowski (1984) has suggested that enhancement of egg production is an important goal in managing these fisheries. A seasonal closure of this fishery during the spawning season would be an effective step to achieving a dual goal of increasing egg production and reducing fishing effort.

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TABLE 1

Values of the v:m ratio and R statistic before, immediately after, and 3 days after a manipulation of the dispersion of H. laevigata in an experimental plot at Waterloo Bay on 27 October 1983. The dispersion pattern (regular, random or aggregated) is shown for each with results of significance tests (\*P < 0.05; \*\*P < 0.01; \*\*\*P < 0.001).

Plot = experimental plot.

Site	Date	Mean density (nos m <sup>-2</sup> )		v:m ratio		R statistic		
		≥ 120 mm	Total popn.	≥ 120 mm	Total popn.	< 100 mm	≥ 120 mm	Total popn.
Plot	27/10/83	0.33	0.78	1.41 Agg**	1.22 Rand.	0.82 Rand.	0.64 Agg**	0.83 Rand.
Control	27/10/83	0.63	1.38	2.26 Agg*	0.61 Rand.	1.49 Reg*	0.59 Rand.	1.08 Rand
Plot after manipulation	27/10/83	0.49	0.92	0.22 Reg***	0.45 Reg***	1.51 Reg***	1.59 Reg***	1.55 Reg***
Plot (10 m x 10 m area)	30/10/83	0.60	0.89	1.82 Agg***	1.49 Agg***	0.86 Rand.	0.60 Agg***	0.76 Agg**
Plot <sup>+</sup> (8 x 8 m area)	30/10/83	0.67	0.94	2.03 Agg***	1.48 Agg***	0.90 Rand.	0.53 Agg***	0.54 Agg***
Control	30/10/83	0.88	1.25	1.78 Agg*	1.31 Rand.	0.82 Rand.	0.51 Agg*	0.60 Agg*

+ the 10 x 10 m plot after exclusion of 1 m<sup>2</sup> quadrats from the perimeter.

TABLE 2

Values of the v:m ratio and R statistic before and after a manipulation of the dispersion of H. laevigata in an experimental plot at Waterloo Bay on 27 April 1984. See Table 1 for details.

Site	Date	Mean density (nos m <sup>-2</sup> )		v:m ratio		R statistic		
		≥ 120 mm	Total popn.	≥ 120 mm	Total popn.	< 100 mm	≥ 120 mm	Total popn.
Plot	27/4/84	0.26	0.34	0.98 Rand.	1.00 Rand.	0.94 Rand.	1.09 Rand.	1.20 Rand.
Control	27/4/84	0.13	0.31	0.96 Rand.	2.86 Agg***	0.39 Agg***	0.90 Rand.	0.79 Rand.
Plot after manipulation	27/4/84	0.81	0.89	0.22 Reg***	0.36 Reg***	0.94 Rand.	1.80 Reg***	1.80 Reg***
Plot (10 x 10 m)	30/4/84	0.69	0.89	0.97 Rand.	0.98 Rand.	1.05 Rand.	1.19 Rand.	1.29 Reg**
Plot (8 x 8 m)	30/4/84	0.61	0.80	1.01 Rand.	0.99 Rand.	0.95 Rand.	1.04 Rand.	1.13 Rand.
Control	30/4/84	0.20	0.20	1.00	1.00 Rand.	None	0.79 Rand.	0.79 Rand.

CAPTIONS TO FIGURES

Fig. 1. (upper) Changes in variance : mean ratio for a population of H. laevigata at West I. 1981-1984.

(lower) Changes in R Statistic during the same period. In each graph solid symbols indicate a significant ( $P < 0.05$ ) departure from randomness, and open symbols a random dispersion.

Fig. 2. Changes in R statistic with increasing age. Symbols as in Fig. 1. (lower)

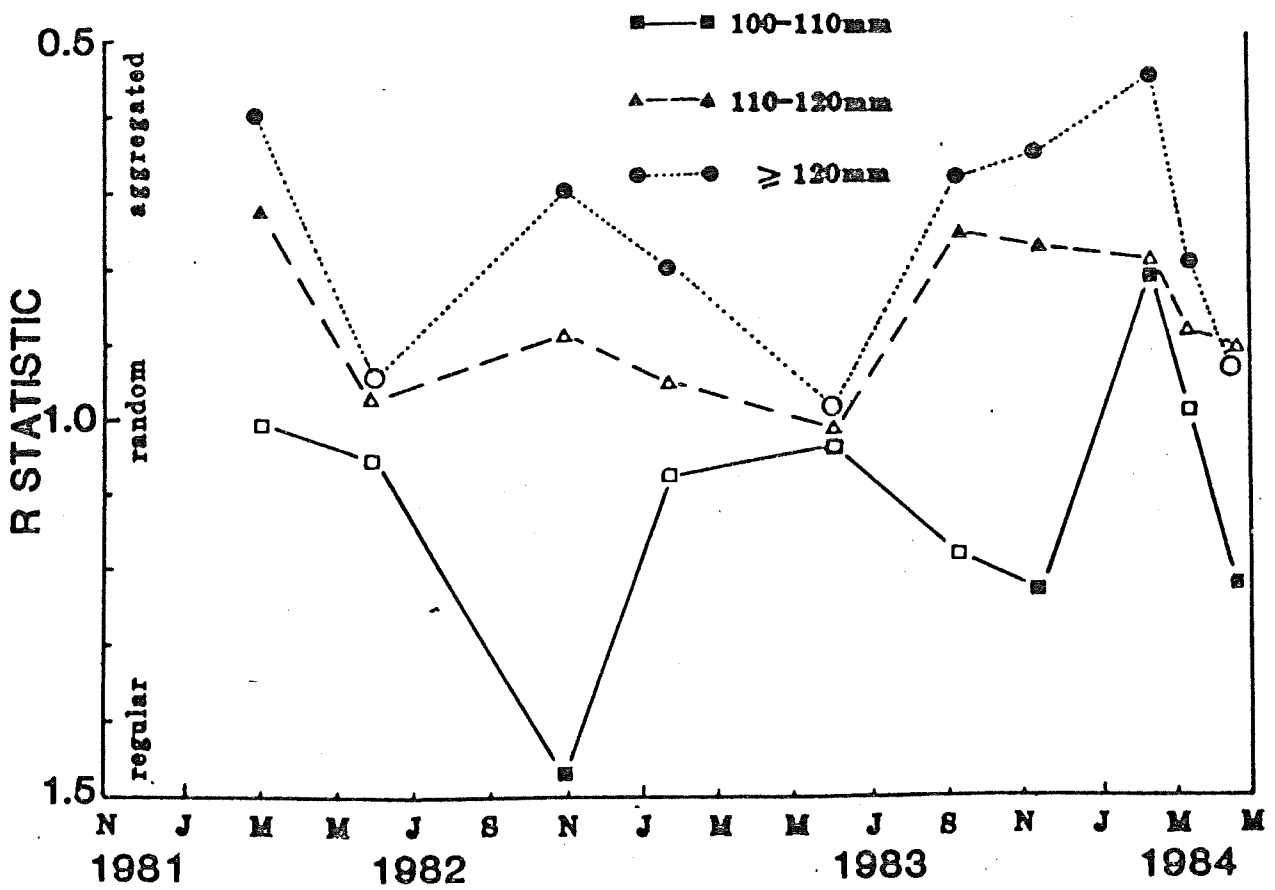
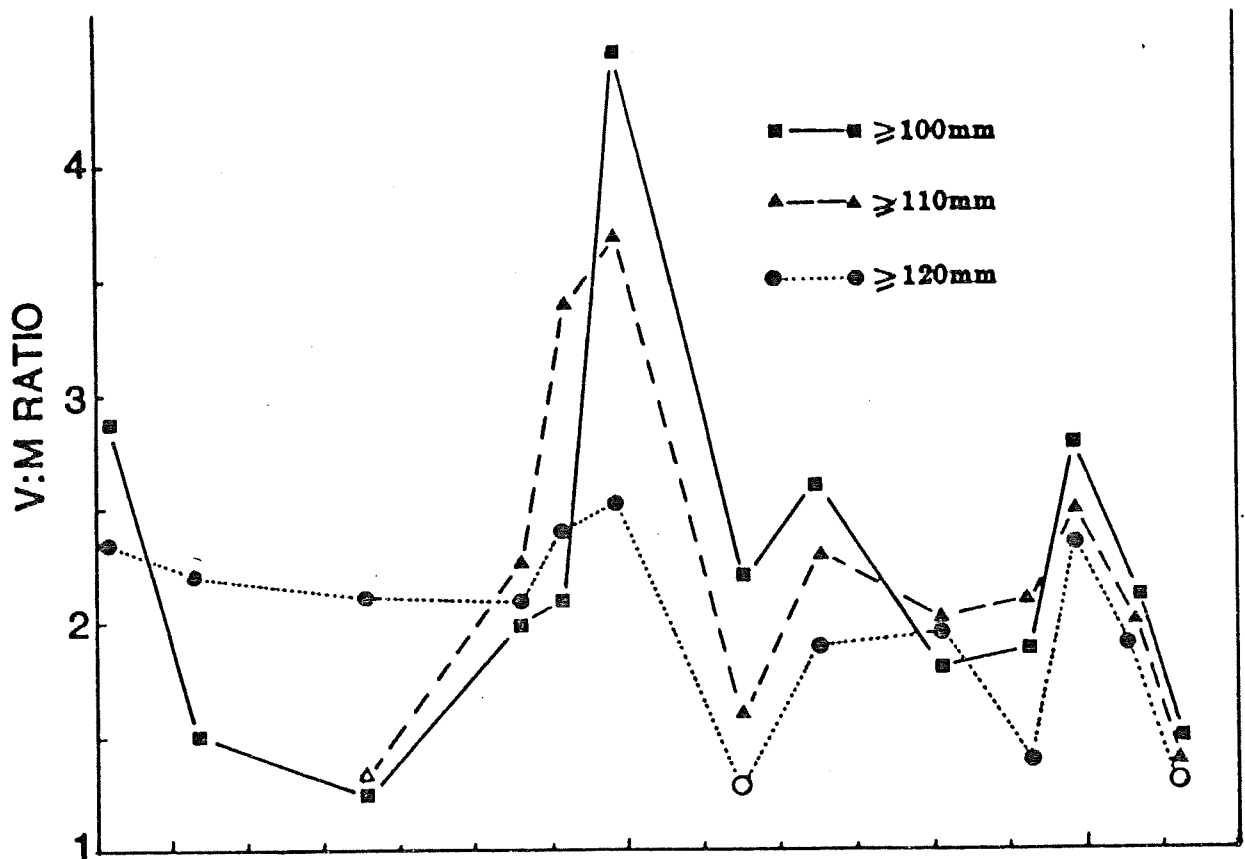
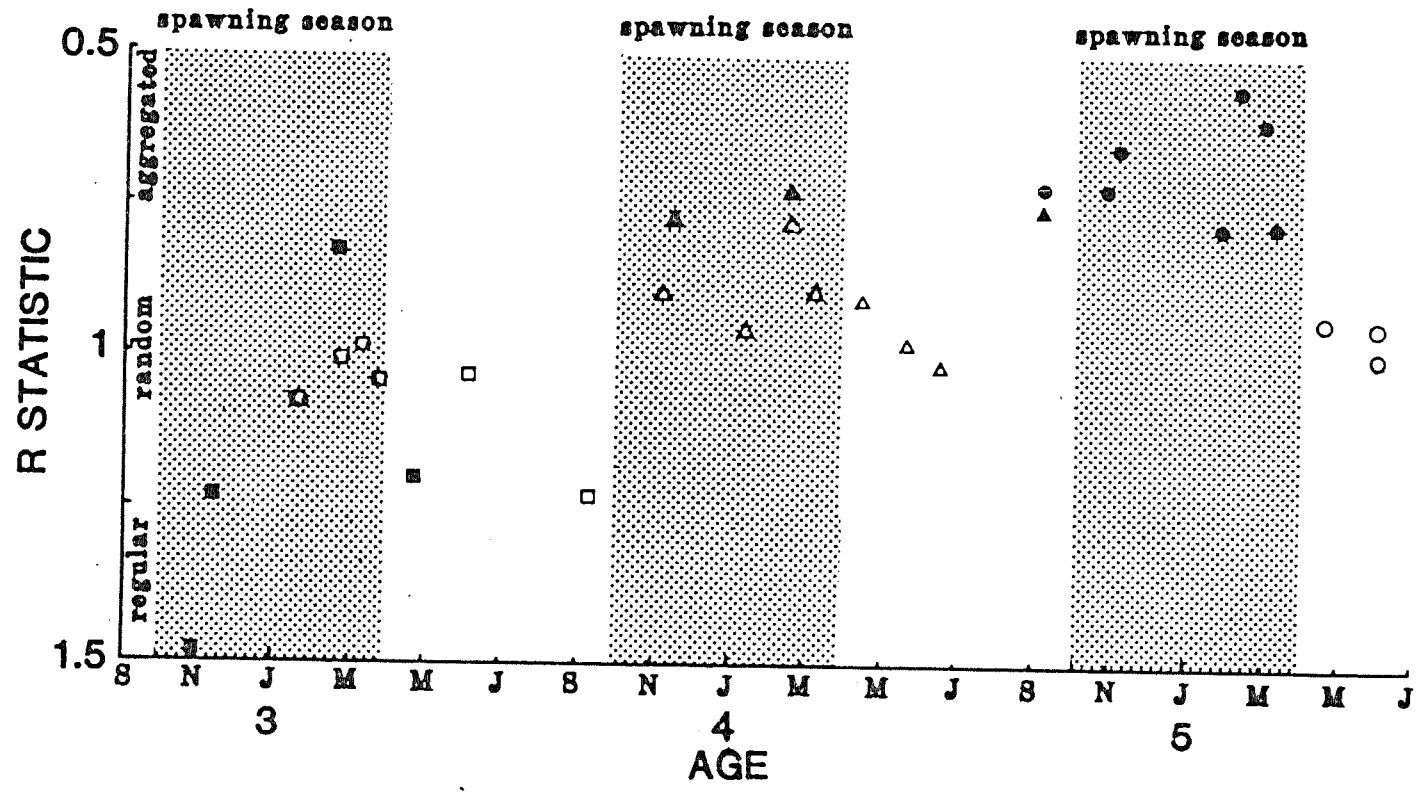


Fig. 1

Fig. 2



APPENDIX 3

Habitat preference, abundance and predators of juveniles.  
(ms submitted to J. Exp. Mar. Biol. Ecol.).



Studies on Southern Australian abalone (genus Haliotis) VII.

Habitat preference, abundance and predators of juveniles.

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ABSTRACT:

The two abalone species Haliotis laevigata Donovan and Haliotis scalaris Leach recruit onto a crustose coralline algal substrate on boulders at West Island, South Australia. Peak settlement of H. laevigata is from December to February, and of H. scalaris from February to June. Recruitment was strong in 1983, but very weak in 1984 when maximum summer sea temperatures were lower. Experimentally placed boulders established the preference of these abalone species for a crustose coralline algal substrate. Wrasses are important predators of juveniles but do not take individuals <5 mm long. The association of juvenile abalone with crustose corallines appears to be important for food and as a refuge from predators. Key words: abalone, larval settlement, recruitment, Haliotis

INTRODUCTION

A critical but poorly known aspect of the life history of most marine invertebrates is the habitat requirements of their newly settled larvae, whose ability to discriminate between different substrates may be crucial to their subsequent survival. An understanding of the habitat needs of larvae of commercially important species such as abalone is basic to the management of natural stocks and to the development of methods for their artificial culture.

Crofts (1929) noted that the smallest individuals of the abalone Haliotis tuberculata Linn. occur on crustose coralline algae, an observation since confirmed for other haliotids (Shepherd 1973; Saito 1981), while laboratory experiments on H. rufescens Swainson and H. fulgens Philippi (Morse et al. 1979 a,b, 1980) have demonstrated that crustose coralline algae induce metamorphosis and settlement of their veligers. However, there have been no previous studies on the natural habitat preferences of newly settled abalone. This paper describes such studies on the greenlip abalone Haliotis laevigata Donovan, taken commercially in southern Australia, and on Haliotis scalaris Leach, a smaller non-commercial species. Both species recruit onto boulders at West Island, South Australia (35°37'S., 138°35'E.) (Shepherd 1973) where a population of H. laevigata has been monitored since 1969 (Shepherd 1985). We describe the microhabitat and abundance of juveniles of these species at 4 - 5 m depth in Abalone Cove over two years. Experimentally placed boulders were used to verify observations on selection of substrate and to determine the relative importance of predation. The size range of young abalone taken by wrasses was obtained directly by field experiments and analysis of gut contents.

#### MATERIALS AND METHODS

A magnifier consisting of two +1650 power (15 diopter) aspheric lenses mounted in a perspex holder (Fig. 1) was used to search for very small abalone. This magnifier differs from the immersion type described by Pratt (1973) by having an air space between the lenses. The magnification underwater is about 2.5 - 3 times. Using this magnifier, we carefully searched the whole of the upper and lower surfaces of boulders at 4-5 m

depth for small abalone and measured their length with vernier calipers. Data were recorded as numbers seen 15 min<sup>-1</sup> searching time. The substrate on which the abalone was found was also recorded.

A number of different microhabitats occur on and under boulders and are described by Kangas and Shepherd (1984). In the present study they are divided into the following categories: erect algae; crustose coralline algae; non-calcified crusts of red and brown algae; encrusting animals (ascidians, bryozoans and sponges); and bare areas. Upper and lower surfaces were also distinguished. Percentage cover data for these categories are from Kangas and Shepherd (1984).

These boulders rest on sand, or on top of other boulders. Sampling was stratified to include both kinds of boulders. Average searching time per census was 93 minutes (40-80 minutes at low densities of < 1 small abalone per 30 min searching time and 80-230 minutes at higher densities), and censuses were at about monthly intervals, or more frequently during the period of maximum settlement.

Erect algae growing on the boulders were carefully removed and placed in plastic bags and later searched for small abalone under a low power microscope (x12 - 25). Densities of adult H. laevigata are higher at the western than the eastern end of the study site, whereas H. scalaris is more or less uniformly scattered throughout the area. Searching was carried out at the eastern and western ends of the area to test for differences in the numbers of small abalone between each area.

On 2 November 1982 an experiment was set up to examine the effect of crustose coralline algae and the natural boulder fauna on the settlement and survival of abalone within a group of 9 island boulder structures. The structures were placed on sandy bottom near the base of the boulder

slope at the study site. Each structure consisted of boulders placed within a metal frame set on a double concrete base designed to let sediment pass through it, (Fig. 2).

Three of the structures contained bare boulders (BB) taken from nearby sandy bottom in which they were buried. Three contained boulders (CC) with crustose coralline algae growing on them, and from which all animals (grazing chitons, and gastropods, terebellid worms, anemones and encrusting bryozoans and sponges) had been removed. The last three contained boulders with their accompanying fauna (CCF). The structures were arranged as shown in Fig. 2. Using the magnifier described above, we searched the upper and lower surfaces of boulders in each structure for small abalone on four occasions between December 1982 and May 1983. We standardised searching time to 15 minutes per structure except for the BB structures, which could be completely searched in about half that time.

The data for each of the searches were considered to be independent because individuals present at one census would have grown out of the size class sought by the next census (Shepherd and Hearn 1983, Shepherd et al, 1985). The results for each treatment were accordingly pooled over time.

## RESULTS

### Natural boulder habitat.

The community on the upper surface of boulders at 4-5 m depth is distinctly different from that below. Above boulders there is an algal community of three strata: an upper stratum mainly of Cystophora monilifera or Ecklonia radiata, a middle stratum of erect geniculate coralline algae (mainly Halptilon roseum, Amphiroa anceps and Cheilosporum elegans) and a crustose stratum of non-calcified brown (mostly Archaeolithoderma sp.) and red

(Cruoria sp.) algae, and crustose coralline algae of the genera: Sporolithon, Lithothamnion, Leptophyton, Mesophyllum, Tenarea and Clathromorphum. On the under-surface of boulders there are crustose algae as described above and crustose ascidians, bryozoans and sponges. Grazing chitons (Kangas and Shepherd 1984), archaeogastropods (Clarkson and Shepherd 1985), terebellids and anemones are also present. The mean percentage cover of algae and of the principal categories of crustose organisms are given in Table 1.

#### Habitat of small abalone

Very small abalone 0.5 - 1 mm long with translucent shells and without poreholes were found on crustose coralline algae. They were sometimes active and moved at speeds of up to 2 - 3 mm sec<sup>-1</sup> on, but never beyond the edge of, the crustose coralline substrate. Possibly disturbance of the boulders during searches provoked this movement.

Two species, H. laevigata and H. scalaris were present on the boulders, but could confidently be distinguished by differences in shell shape only when longer than about 1 mm. A summary of the results of searches for small abalone (<5 mm long) by species and by host substrate from November 1982 to November 1983 in the natural habitat is given in Table 1.

Nearly all (94%) were found on crustose coralline algae either on upper or under sides of boulders or on vertical surfaces. Three were found on non-calcified crusts and none in any other microhabitat. No small abalone were found on any erect algae.

Significantly more were found on the under than the upper sides of boulders ( $\chi^2 = 12.64$ ;  $P < 0.001$ ). However, because crustose corallines have more than twice the total cover on under as on upper sides, the distribution of both abalone species does not differ from that expected under the

hypothesis of random settlement on crustose corallines according to cover (for *H. laevigata*  $\chi^2 = 1.93$ ;  $P > 0.05$  and for *H. scalaris*  $\chi^2 = 1.15$   $P > 0.05$ ). The position of four *H. laevigata* on boulders was not recorded (Table 1) but even the extreme assumption that they were all from the upper side made no difference to the conclusion ( $\chi^2 = 2.94$ ;  $P > 0.05$ ). We have assumed that differential mortality between upper and under sides did not occur, because data on wrasse predation (see below) showed that no individuals  $< 5$  mm long were taken.

To test whether more juvenile *H. laevigata* settled near conspecific adults we examined two subsets of the data in Table 1 taken from areas of high ( $3 - 4 \text{ m}^{-2}$ ) and low ( $0.5 - 1.5 \text{ m}^{-2}$ ) adult mean densities. After minor adjustment to equalise searching time, 53% of juvenile *H. laevigata* were found in the low density area and 47% in the high density area. The hypothesis that juveniles were present in equal numbers in the two areas was accepted ( $\chi^2 = 0.17$ ; n.s.), and it was concluded that the relative abundance of adult conspecifics does not influence density of settling *H. laevigata*.

At a length of about 5 - 7 mm *H. laevigata* moves from crustose coralline surfaces of boulders to the undersides of boulders partly buried in sand. In contrast, *H. scalaris* remains on crustose corallines until it is 15 - 20 mm long. This explains why length frequency distributions for the two species (Fig. 3) rarely record *H. laevigata* at a length greater than 5 mm. A similar change in micro-habitat at about this size was noted for a haliotid by Saito (1981). No small abalone  $> 3$  mm long was found on the upper sides of boulders, suggesting that by this size they seek a more shaded crustose coralline surface.

In the experimental structures 26 individuals were recorded on CC boulders, 43 on CCF boulders and 2 on the BB boulders (Table 2). Both of the latter were found on small ( $< 1 \text{ cm}^2$ ) patches of crustose corallines which had grown after the experiment had commenced.

The null hypothesis that the total number of animals found in each type of structure was equal was tested and rejected ( $\chi^2 = 36.5$ ;  $P < 0.001$ ). For this test we standardised the census data as numbers found  $15 \text{ min}^{-1}$  and considered the 4 time periods as replicates. We then tested whether the number found on the CCF boulders differed significantly from that on the CC boulders and rejected the hypothesis of equality of numbers ( $\chi^2 = 4.21$ ;  $P < 0.05$ ). Lastly we tested whether the abundance of juveniles (in numbers  $15 \text{ min}^{-1}$ ) was greater in the boulder structures (CC and CCF pooled) than on the natural boulder slope. Significantly more occurred in the structures than among the natural boulders than expected from the relative searching times ( $\chi^2 = 18.5$ ;  $P < 0.001$ ).

#### Abundance of small abalone

The size distribution of H. laevigata and H. scalaris at each sampling date from November 1982 to July 1983 is shown in Fig. 3. These data include the results of sampling the natural boulder habitat as well as the structures. The presence of individuals 0-2 mm long is accepted as indicative of recent settlement; this is based on a growth rate of about 1 mm per week for H. laevigata (Shepherd and Hearn 1983) and 0.4 mm per week for H. scalaris (Shepherd et al. 1985). On this basis settlement of H. laevigata occurred from November 1982 through to May 1983, and settlement of H. scalaris from January through to June 1983. The period of settlement of both species closely accords with their respective spawning seasons (see Shepherd and Laws (1974) for H. laevigata and Shepherd et al. (1985) for H. scalaris).

A plot of the numbers of small abalone <5mm recorded per 15 min searching time (Fig. 4) gives a measure of the relative strength of settlement of both species in 1983 and 1984. For this purpose unidentified individuals <1mm long were assigned to the two species in proportion to the relative abundances of larger individuals (1 - 5 mm long) at that sampling date. The possibility of error here is slight, because the numbers in this category were low during the period of settlement overlap.

Settlement of H. laevigata was strong in 1982-83 (peaking in November 1982) and weak in the following settlement season. Similarly settlement of H. scalaris was relatively strong in the 1983 season and not detected at all in 1984.

#### Predation on small abalone

Two principal predators of small abalone are the wrasses Pseudolabrus tetricus (Richardson) and Pictilabrus laticlavus Richardson (Shepherd and Clarkson in prep.). The various fish, crustacean and molluscan predators of small abalone listed by Shepherd (1973) and other potential predators like flatworms are rare or absent at the study site at West Island. Possible predation by nemertean has not yet been evaluated.

We attempted to assess the effect of fish predation on abundance of small abalone by caging boulders or placing net coverings over them. Two pilot experiments were conducted each for 2 months in 1983 and 1984. At the conclusion of each experiment fewer small abalone were found in the covered boulders than in the uncovered (in one experiment significantly fewer: Mann Whitney, U test,  $P < 0.05$ ), results converse to those expected.



A continual problem, peculiar to situations of strong swell and abundant algal drift, was the accumulation of trapped drift algae and sediment in the covered boulders (despite regular cleaning). We concluded that the results obtained were probably an artifact of the changed environment. Partially covered boulders as cage controls were unsatisfactory because they became the residence of several species of fish. Schmidt and Warner (1984) experienced similar problems with cages. Caging was therefore abandoned in favour of studies on the feeding and prey size preferences of the wrasse P. tetricus.

In experiments conducted during monitoring of the boulder community, boulders were overturned and the small abalone under them were measured. P. tetricus was then allowed to search the exposed underside of the boulder and select prey abalone. Data on the size range of abalone (a) not taken, (b) taken and (c) the object of an unsuccessful attack for different size classes of wrasse are given in Fig. 5.

P. tetricus is a visually searching predator and takes abalone predominantly in the size range 10-30 mm. Abalone <10 mm are rarely taken presumably because their cryptic colour provides camouflage and protection. Some of the smallest ones taken were not on the crustose coralline and this probably facilitated recognition. Analysis of gut contents of 62 P. tetricus (Shepherd and Clarkson in prep.) showed that small individuals 15-20 cm long took gastropods with a mean size of 4.5 mm (s.e. 1.5 mm). However these gastropods lived among the algal turf where the wrasse foraged for amphipods which comprised most of the diet, and so were presumably taken incidentally. The only abalone found in the gut of P. tetricus was 6.5 mm long. However, we cannot infer from this that abalone are rarely taken because the wrasses whose guts were analysed were taken away from the study site, in places where abalone were less frequent.

We conclude that predation by this wrasse on abalone <5 mm long is a rare event.

The wrasse P. laticlavus is a cryptic species and shy of divers and it was not possible to test its visual acuity experimentally in the field. However, it has a similar diet to P. tetricus (unpublished data) and our conclusions for the latter species should apply to it also.

#### DISCUSSION

Our data and observations show that to a size of at least 5 mm these two species of abalone are largely restricted to a crustose coralline substrate. The smallest individuals we recorded had a shell length of about 0.5 mm, when the shell was colourless and lacked pore-holes. Numerous studies (see review by Koike 1978) have shown that the shell develops within 1-4 days of larval settlement and pore-holes appear within another 20 - 30 days, when the shell is around 2 mm long (Leighton 1974; Koike 1978). Shells acquire a pink colour during this period as feeding on crustose corallines proceeds (Morse et al. 1980; Kitting and Morse in prep.). Our observations of the smallest individuals are therefore likely to have occurred within the first two weeks or so of larval settlement. Because small abalone are highly mobile we cannot strictly infer settlement behaviour from later observations. However, the following considerations suggest that our conclusion on substrate specificity of small abalone can be extrapolated back to the time of larval settlement.

Following Underwood (1979) three explanatory models of abalone larval behaviour can be postulated:

- (1) they settle preferentially on crustose coralline algae, or
- (2) they settle haphazardly and then migrate to a crustose coralline substrate, or
- (3) they settle haphazardly and differential mortality eliminates them from other substrates.

The most likely cause of differential mortality is selective predation in unsuitable habitats. The only known predators of abalone larvae are terebellid polychaetes, certain copepods and nematodes (Morse et al. 1979b, Ebert and Houk 1984). Of these, we only saw terebellids under boulders and in particular among the CCF boulders. Another possible predator might be the anemone Anthothoe albocincta (Stuckey) (see Sebens and Koehl 1984) also present among these boulders. But in the experimental structures significantly greater numbers overall of small abalone were found in the CCF boulders with these predators than in those without (CC boulders) suggesting that predation by these sessile species is minor. Similarly, our data on wrasse predation show that abalone <5 mm long are unlikely prey. Consequently the third model of larval behaviour (haphazard settlement and differential mortality) seems unlikely.

The second model (haphazard settlement and migration) is excluded by the absence of small abalone on the bare boulders in the experimental structures.

From this we conclude that the substrate specificity of small abalone is most plausibly explained by substrate preference of the settling larvae. This is supported by the numerous studies of Morse and associates (Morse and Morse 1984) in which they demonstrate preferential settlement of abalone larvae on crustose coralline algae and offer a molecular basis for such preference. They found that  $\gamma$  - amino butyric acid (GABA) and its analogues are agents (chemical signal) inducing metamorphosis behaviour and settlement of competent larvae of Haliotis rufescens Swainson and H. fulgens, Philippi. Only certain crustose red algae have GABA mimetic molecules available at their surface, and so account for the contact dependent and substrate specific settlement of abalone larvae.

The role of crustose red algae inducing settlement of, or as a preferred substrate for, abalone larvae has not been tested outside the laboratory and this study is the first such field investigation.

The association between small abalone and crustose coralline algae is significant in two ways:

- (1) the combination of a smooth substrate (at the scale of a newly settled abalone) providing maximum adhesion for the foot, a shaded surface and cryptic colouration of the abalone constitutes an effective defensive strategy against visually searching predators.
- (2) The mucous exudate from the crustose corallines (Giraud and Cabioch 1976) may, and epiphytic diatoms do, provide a source of food for newly settled abalone (Kitting and Morse in prep.; and see review by Shibui, 1972). This resource is also shared by chitons and archaeogastropods (Kangas and Shepherd 1984; Clarkson and Shepherd, 1985) but is unlikely to be limiting, at least at our study site because of the low densities of molluscs found.

There may also be a reciprocal benefit to the crustose coralline by the abalone removing fouling epiphytes (Adey 1973; Steneck 1977; Paine 1980; Kitting and Morse in prep.) but this possibility needs further investigation.

There is some evidence that the association with crustose coralline algae may not be universal among all abalone species, or there may be other cues involved in larval settlement. For example in experiments with veligers of H. discus hannai Ino, Momma (1973) found that maximum settlement occurred on certain diatom films, while Seki and Kanno (1981 a,b) showed that the mucous trails of adult abalone induced settlement. However in our case, lack of any significant difference in the abundance of juvenile H. laevigata between areas of high and low adult density discounts the likelihood that larvae are attracted to or by conspecific adults. But, the possibility that 1 and 2 year old conspecifics, which are more mobile than adults (Shepherd 1973) and thus are likely to leave trails, attract settling veligers needs investigation.

Studies of abalone recruitment have been hampered in the past by the lack of a quantitative technique to measure strength of larval settlement. The CCF experimental structures used in this study were more effective than both the natural boulder habitat and the CC structures in terms of densities of young abalone recorded (Table 2). One of the several factors which may have contributed to these differences is the progressive decline of crustose coralline cover through overgrowth on the CC structures due to absence of grazing (Clarkson and Shepherd 1985). Thus, if a healthy crustose coralline substrate can be maintained, the experimental structures offer a simple, replicable, uniform technique to measure settlement strength of abalone larvae in time or space.

This paper adds to a growing list of species in four phyla which are thought to settle selectively on crustose coralline algae. In addition to numerous haliotids the list now includes three species of chiton (Barnes and Gonor 1973, Morse et al. 1979 a, Rumrill and Cameron 1983), a trochid (Heslinga 1981), a spirorbid worm (Gee 1965), a limpet (Branch 1975), an octocoral (Sebens 1983), a scleractinian coral (Harrigan 1972) and a seastar (Barker 1977). Thus this relationship between animal and a family of plants has apparently evolved independently in different places among different species. The benefits to the animal are functional i.e. the substrate serves as a food resource, a refuge, or an indicator of suitable habitat. An intriguing question for future research is whether the relationship is species-specific i.e. whether settling larvae can discriminate between crustose coralline taxa and so further identify an optimal habitat.

#### ACKNOWLEDGEMENTS

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Table 1 Percentage cover of organisms above and below boulders at 5 m depth in Abalone Cove, West Island, and numbers of *H. laevigata* and *H. scalaris* <5mm recorded in each microhabitat from November 1982 to November 1983.

	Boulder Under Surface				Boulder Upper Surface				Vertical rocky surfaces with crustose corallines)	Crustose corallines. Position on boulder not specified.
	Crustose corallines	Non-calcified crusts +	Bare rock	Other*	Geniculate corallines and erect algae	Crustose corallines	Non-calcified crusts	Bare rock		
mean % cover	34	9	47	9	28	13	50	3	100	
s.e.	0.7	0.5	0.9	0.6	2.1	1.6	3.1	-		
<i>H. laevigata</i>	29	1	0	0	0	6	1	0	2	4
species uncertain	2	0	0	0	0	1	0	0	0	0
<i>H. scalaris</i>	13	0	0	0	0	8	1	0	0	0

\* bryozoans, ascidians, sponge.

+ these crusts are mostly an undescribed species of *Archaeolithoderma* (Phaeophyta) but include species of *Cruoria* (Rhodophyta) and probably other genera.

Table 2

Numbers of small abalone (< 5 mm) and searching time (in minutes) on 9 experimental structures at West Island. BB = bare boulders. CC = boulders with crustose corallines only. CCF = boulders with crustose corallines and other under boulder fauna.

Date							Mean Density	
	BB	Time	CC	Time	CCF	Time	Exper. Structure	Natural Habitat
21.12.82	0	55	5	70	13	70	3.0	3.2
17. 1.83	2*	30	11	60	12	60	3.8	0.9
15. 2.83	0	45	7	60	9	80	1.7	0.8
18.5.83	0	20	3	50	9	50	1.8	0.2
TOTAL	2	150	26	240	43	260		

\* found on small patches of crustose corallines

+ Mean density (in numbers recorded per 15 min searching time) are for CC and CCF habitats only.

#### Captions to text figures

Fig. 1 Diagrammatic cross-section of magnifier for underwater use.

Fig. 2 (Upper) photograph of experimental structure (60x60 cm) at West Island. Note holes in upper concrete slab allowing trapped sediment to pass through the habitat. (Lower) Arrangement of structures.

Fig. 3 Length frequency distributions of small H. laevigata and H. scalaris from November 1982 to August 1983.

Fig. 4 Density (in numbers found per 15 minutes searching time) of small H. laevigata (circles) and H. scalaris (triangles) at Abalone Cove, West Island from October 1982 to June 1984.

Fig. 5 Size range of small abalone not taken, taken, or unsuccessfully attacked by different length classes of the wrasse P. tetricus. Discontinuous lines indicate the approximate upper and lower boundaries of size range of abalone taken.

Fig. 1

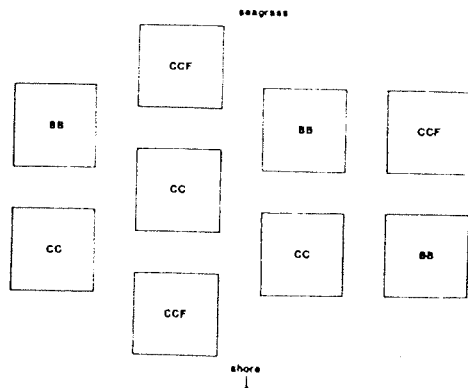
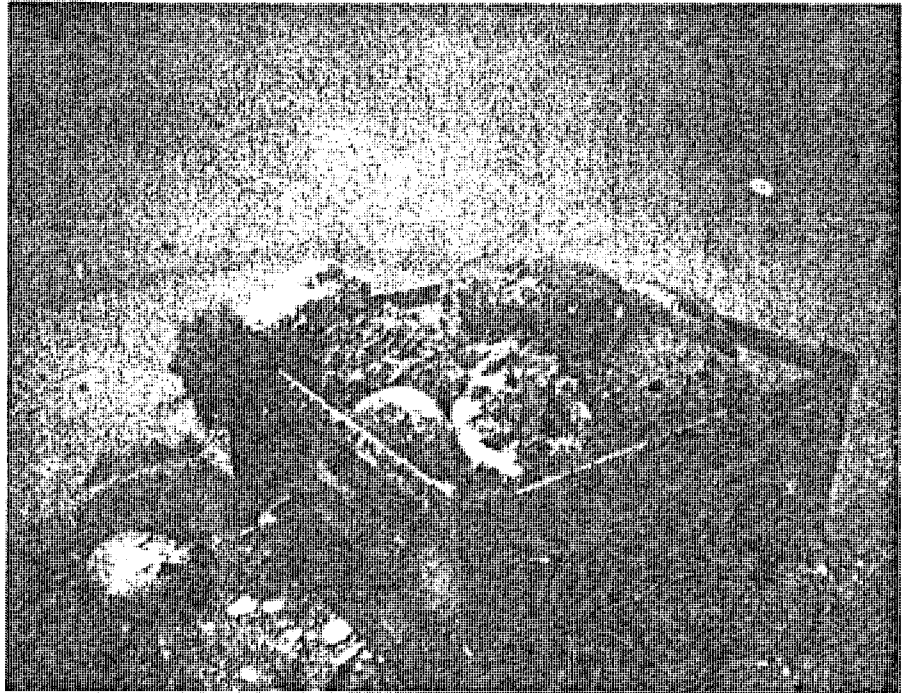


Fig. 2

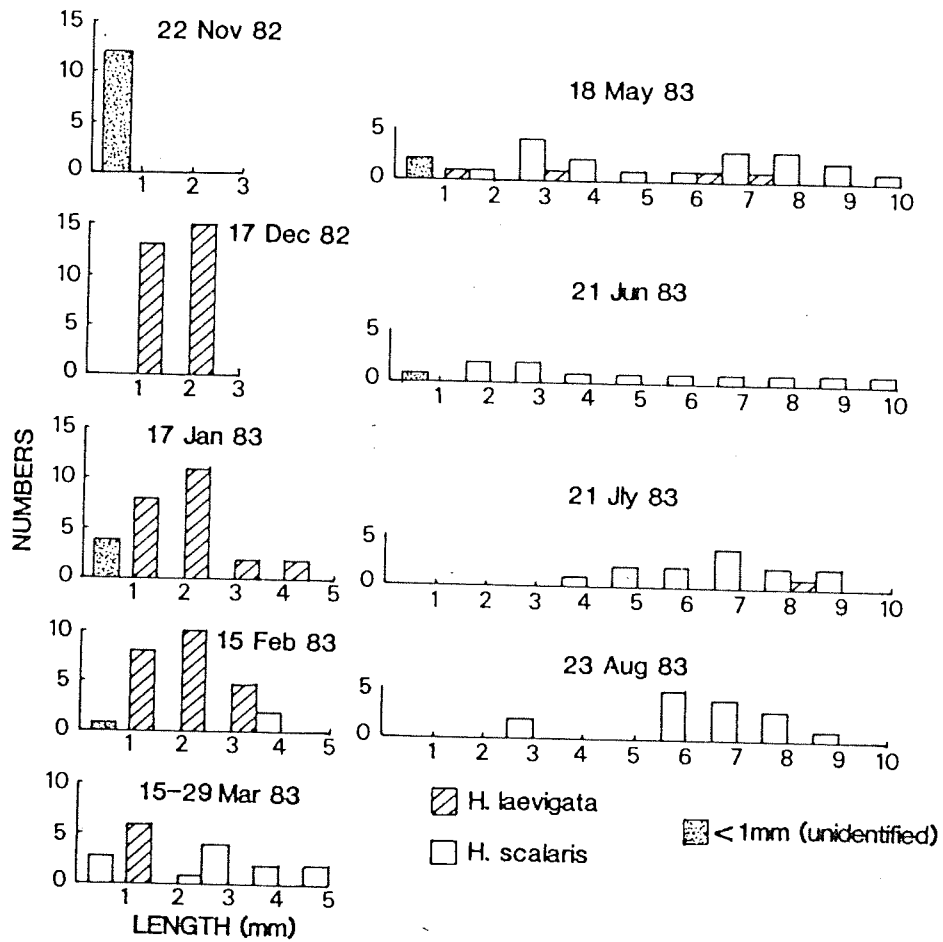


Fig. 3

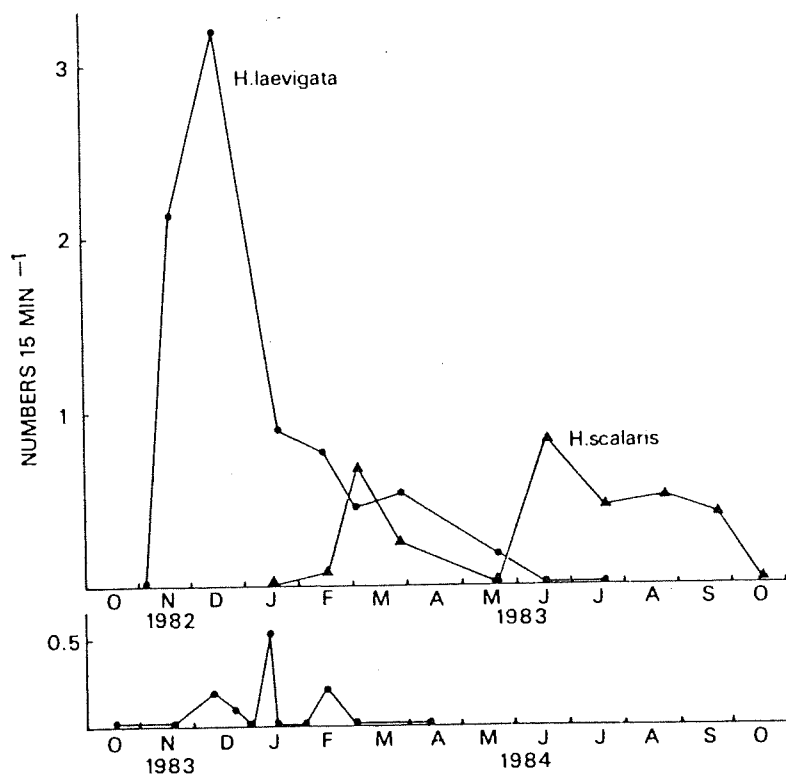


Fig. 4



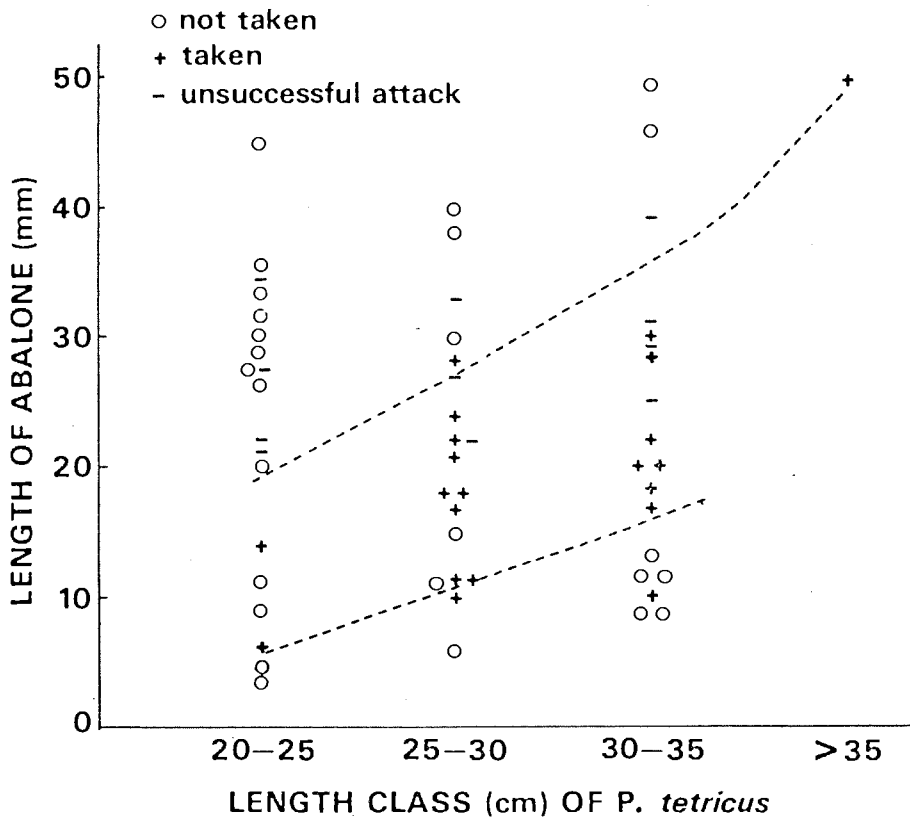


Fig. 5

APPENDIX 4

Spawning, settlement and early growth of H. scalaris.  
R. Soc. S. Aust. (in press).

BRIEF COMMUNICATION

STUDIES ON SOUTHERN AUSTRALIAN ABALONE (GENUS *HALIOTIS*) V.  
SPAWNING, SETTLEMENT AND EARLY GROWTH OF *H. SCALARIS*

This note describes the spawning cycle of *Haliotis scalaris* Leach and the settlement density and growth of juveniles of the species at West Island (35°37'00"S, 138°35'00"E), South Australia. This spawning cycle differs markedly from that previously described for the species at Tiparra Reef, South Australia and is therefore of considerable interest.

Samples of 9-12 sexually mature female *H. scalaris* 65-80 mm long were collected at Abalone Cove, West I., at about monthly intervals from February 1983-July 1984. The entire visceral mass was preserved in 10% formalin and sea-water and later sectioned in the laboratory. Cross-sections of the gonad and digestive gland were traced on transparent plastic, the cut-out sections weighed, and the respective areas of gonad and digestive gland calculated. A gonad index was then calculated with the formula Gonad index = 100 (Area of gonad / Total area of section). The annual reproductive cycle of this species at West I. proved to be synchronous within the population, so that measurement of oocyte-ova diameters to distinguish the stages of the reproductive cycle was unnecessary (see Shepherd & Laws<sup>1</sup> for details of the method).

Sea surface temperature data were obtained with a mercury thermometer at about monthly intervals at West I.

A hand lens, designed for use underwater with about 3x magnification (the optics are described by Shepherd & Turner in prep.) was used to search for *H. scalaris* on crustose coralline algal substrate, the preferred substrate for settlement of this species (Shepherd & Turner in prep.). Searches were done for 60-100 minutes at about monthly intervals in the boulder habitat at West I. at 4-5 m depth and the lengths of all individuals to about 25 mm long recorded to 0.1 mm.

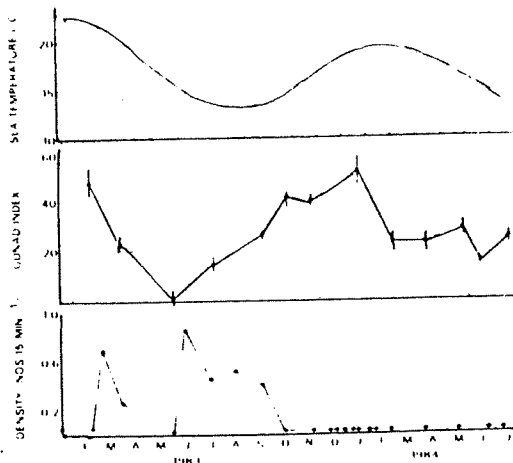


Fig. 1. (upper)—mean monthly sea surface temperatures (smoothed curve); (mid)—monthly distribution of gonad indices with standard errors; (lower)—density of small *H. scalaris* < 5 mm at study site.

Changes in the mean monthly gonad index of *H. scalaris* from February 1983-May 1984, together with sea surface temperature data are given in Fig. 1. The index increases from winter to mid-summer and declines abruptly from late summer through the autumn. The increase indicates maturation and increase in size of oocytes in the gonad, and the decline of the index indicates the onset of synchronous spawning in the population. Spawning appears to have commenced later in 1983 than in 1984 and to have been more complete. In 1984 the gonad never became completely spent but commenced to increase in size again in July.

Thus *H. scalaris* has a late summer to autumn spawning season (February-May) which is synchronous throughout the population, and appears to begin at about the time of maximum summer sea temperature. This spawning cycle contrasts strikingly with the asynchronous cycle of *H. scalaris* at Tiparra Reef where spawning potentially occurs throughout the year.

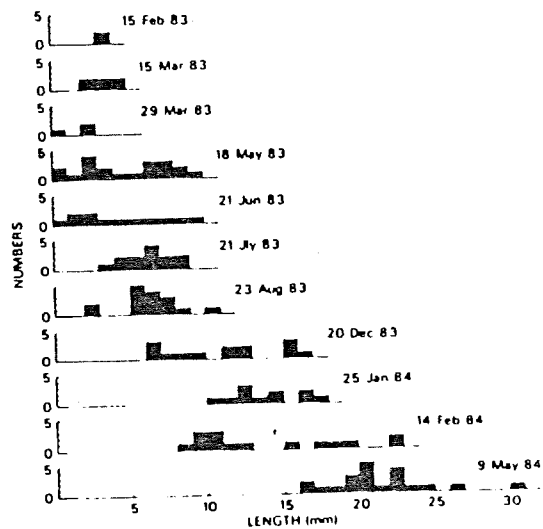


Fig. 2. Length frequency distributions for *H. scalaris* at West Island from February 1983 to May 1984.

Of the various environmental factors that are known to influence the spawning cycles of abalone e.g. temperature,<sup>2</sup> photoperiod,<sup>3</sup> and food abundance<sup>4</sup> only the latter shows a marked difference between the two sites. Drift food algae are seasonally in short supply at Tiparra Reef but abundant throughout the year at West I.,<sup>5</sup> but this is unlikely to account for the differences in spawning between the sites. Further studies of *H. scalaris* are necessary, especially in other parts of its geographic range, to elucidate the problem. *H. rubra* Leach also shows marked, but unexplained, differences in spawning cycle between these two sites.<sup>1</sup> The only other abalone species that we know of with a similarly variable spawning cycle between localities is *Haliotis rufescens* Swainson.<sup>6,7</sup>

The density of small *H. scalaris* (measured in mean numbers of individuals  $\leq 5$  mm recorded per 15 min searching time is given in Fig. 1. Maximum settlement apparently occurred in March 1983. The relatively high densities recorded from July to September 1983 are of larger individuals (3-5 mm) and do not indicate recent settlement.

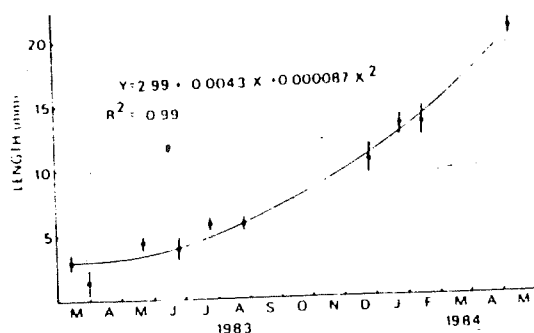


Fig. 3. Plot of mean length (with standard errors) of 1983 cohort of *H. scalaris* from March 1983 to May 1984. A polynomial regression of best fit to the means is shown.

Length frequency data from February 1983-May 1984 (Fig. 2) show that very small *H. scalaris* (1-3 mm long) were present from February-June 1983 indicating

settlement in that period. This is in good agreement with the spawning season described above. No small *H. scalaris* were found in the 1984 spawning season, suggesting settlement was very poor and not detectable.

Shepherd (in prep.) associated the similar poor recruitment of *H. laevigata* Donovan at West I. in 1984 with the lower maximum summer sea temperature in 1984 compared with 1983. The settlement failure of *H. scalaris* in 1984 may also be associated with lower summer sea temperatures in that year or with the incomplete spawning or a combination of them.

The change in mean size of the 1983 cohort from March 1983-May 1984 (Fig. 2) enables an estimate to be made of the growth of the cohort in the first year. The equation of best fit empirically fitted to the data is given in Fig. 3. On the basis that settlement occurred between 1 February and 30 June 1983, a mean birth date for the cohort can be fixed at 15 April 1983. From the regression (Fig. 3) the mean length of the one year old animal is therefore about 18.5 mm. Comparison of this growth rate with that of other haliotids<sup>6</sup> suggests that it is relatively rapid for a species whose maximum size (at West I.) is only about 100 mm.

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- <sup>1</sup>Shepherd, S. A. & Laws, H. M. (1974). *Aust. J. Mar. Freshw. Res.* 25, 49-62.  
<sup>2</sup>Kikuchi, S. & Uki, N. (1974). *Bull. Tohok. Reg. Fish. Res. Lab.* 33, 69-78.  
<sup>3</sup>Kim, Y. & Cho, C. (1976). *Bull. Korean Fish. Soc.* 9, 61-68.  
<sup>4</sup>Giiese, A. C. (1959). *Ann. Rev. Physiol.* 21, 547-576.

- <sup>5</sup>Shepherd, S. A. (1973). *Aust. J. Mar. Freshw. Res.* 24, 217-257.  
<sup>6</sup>Giorgi, A. E. & De Martini, J. D. (1977). *Calif. Fish and Game* 63, 80-94.  
<sup>7</sup>Lee, T. Y. (1974). *Publ. Mar. Lab. Busan Fish. Coll.* 7, 21-50.  
<sup>8</sup>Shepherd, S. A. & Hearn, W. S. (1983). *Aust. J. Mar. Freshw. Res.* 34, 461-75.

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APPENDIX 5

Distribution and feeding of archaeogastropods in  
a boulder habitat at West I., South Australia.  
J. Malac. Soc. Aust. (in press).

# Distribution and feeding of archaeogastropods in a boulder habitat at West Island, South Australia

by P.S. Clarkson and  
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## ABSTRACT

SK

The vertical distribution and feeding of eleven species of archaeogastropods were examined on a boulder slope at West Island, South Australia. Most species occur throughout the depth range, but species which feed on drift seagrass and algae occur in higher density at about 4m depth.

All species are herbivorous and feed variously on geniculate and crustose coralline algae, *Petroderma* crusts, macrophytes and drift seagrass and algae. There are minor differences between the species in microhabitat and type of food eaten.

Removal experiments show that, in the short term, these archaeogastropods (together with chitons) control the growth of filamentous algae on the upper sides of boulders.

## INTRODUCTION

Subtidal boulders contain a complex community of erect and crustose algae, crustose animals and mobile grazing and predatory animals. Herbivorous molluscs in particular, play an important role in regulating benthic algal structure by controlling algal growth (Luckens 1974, Lubchenko 1978, Raffaelli 1979, Brawley and Adey 1981, Underwood and Jernakoff 1981). In order to elucidate the mechanisms controlling such a complex system it is necessary first to identify functionally similar groups of organisms and then to discover their effect by manipulations. This paper primarily addresses the former of these objects. It describes the distribution and feeding of some archaeogastropod molluscs in a subtidal boulder community, at West Island, South Australia and adds to an accumulating corpus of information on its biology, e.g. the algal communities (Shepherd and Womersley 1970), grazing by a chiton guild (Kangas and Shepherd 1984), and ecology of abalone (Shepherd 1973, Shepherd and Turner in prep.).

## MATERIALS AND METHODS

The north shore of Abalone Cove, West Island, (35° 36' 25" South; 138° 35' 27" East) is a boulder slope with boulders, mostly 30 - 40 cm x 20 - 30 cm, and 20 cm high from about 0.5m depth to 5m at low water. At six depth intervals, 0.5m and from 1 to 5m at 1m depth intervals, 10 boulders were thoroughly examined, and the archaeogastropods (excluding limpets) on both the boulder upper and under surfaces, and on rocks below the boulder, identified and counted. This survey was conducted in March 1983 and again in September 1983. In order to estimate the density of archaeogastropods, the area of each boulder was taken to be its projection on the horizontal plane.

Archaeogastropods were collected between May and September 1983, and preserved in 10% formal sea-water. The stomach contents of samples of each species were extracted and spread out on a slide or petri dish for microscopic examination. The contents were scanned along several parallel lines, and the material under the cross of the eyepiece at equidistant points identified to morphological group.

Plant material was categorised as coralline algae (geniculate and encrusting), *Petroderma* crusts\*, filamentous algae, brown, red or green macroalgae, and seagrasses, in accordance with the functional group approach of Steneck and Watling (1982).

A night dive was made on 21/6/83, and the presence or absence of normally cryptic species on the upper surfaces of boulders noted.

Percentage similarity (Bray and Curtis 1957) between the diets of 11 species was calculated and a dendrogram grouping species by the nearest neighbour method (Field and McFarlane 1968) was used to discover associations in terms of diet between species.

In a short term manipulation four experimental structures were set up on sandy bottom adjoining the subtidal boulder slope on 19 September 1983. Each structure consisted of a concrete base and 10 - 15 boulders all contained within a metal frame. The boulders were covered with crustose corallines and *Petroderma* sp., but all grazing animals (archaeogastropods and chitons) were removed from them. The controls were boulders which remained undisturbed at the base of the boulder slope and were subject to grazing by gastropods and chitons. We did not specifically control for disturbance of boulders because other experiments concurrently in progress showed that similar structures of boulders but with grazing molluscs on them, remained in the same condition in terms of algal cover as natural boulders.

The growth of erect algae on boulders was sampled by carefully taking the boulder from the water and scraping off the algae and trapped sediment on the upper surface from an area of 25cm<sup>2</sup>, with four replicates on different boulders. Algae were dried at 50°C for 24 hours to give dry weight biomass.

\* refers to non-calcified algal crusts mostly of the genus *Petroderma*.

## RESULTS

The distribution of macro-algal communities described by dominance criteria, on the boulder slope in Abalone Cove is given in Fig. 1. Above and below boulders crustose red and brown algae, encrusting sponge, bryozoans, and ascidians (see Kangas and Shepherd (1984) for detailed distributional data) are abundant throughout the depth range.

Seventeen species of archaeogastropods (excluding limpets and abalone) were recorded on the boulder slope. Information on depth range, mean density, size range, and number of gut contents of species analysed are given in Table 1; six of the species were too rare to allow a study of their feeding. The depth distribution and density (averaged for the two surveys) of the 11 commoner species above and below boulders are given in Fig. 2.

Only three of the species (see Fig 2) occur on the upper, as well as under, surfaces of boulders during daylight hours. No additional species were recorded on the upper surfaces of boulders during the single night dive.

Two species showed substantial differences in abundance between the March and September census (Fig. 3). The *G. preissiana* population was mainly juveniles in September and adults in March, implying a recruitment at 4 - 5m depth and later upward migration. *D. odontis* tends to occur in clusters and the differences in Fig. 3 may be a sampling artifact.

The proportional abundance of different food types in the gut of 11 species is shown in Fig. 4. All species are herbivorous, with several food types commonly present in the gut. In some species small amounts of animal matter (mostly sponge but forams in the case of *P. ventricosa* and *G. imbricata*) are present in the gut, and are probably taken incidentally.

The dendrogram (Fig. 5) showing dietary similarities between species discloses several species groupings, some of which coincide with microhabitat differences between species. In general there is high overlap in diet between groups.

The first group, *G. preissiana*, *C. plebejus* and *E. asperus* shares the same microhabitat on the underside of boulders and feeds mainly on sea-grass and crustose coralline algae. Extensive *Posidonia* beds and occasional patches of *Heterozostera tasmanica* occur on adjoining sandy bottom, and drift blades of these seagrasses and algae are abundant under and between boulders.

These species feed on drift, but not living, seagrasses. Except for *G. preissiana*, which eats considerable amounts of *Zonaria* spp. (27%), they eat little macroalgae.

The second group *T. undulatus*, *T. torquatus* and *P. ventricosa* live on the upper sides of boulders (except small *P. ventricosa*) and graze mostly on macrophytes and geniculate coralline algae (mostly *Haliptilon* spp.) The macrophytes eaten differ according to species. *T. undulatus* feeds on *Ecklonia*, (28%) on whose fronds it is commonly found, and green algae of the genus *Caulerpa* (27%). The other species take mostly brown algae of the genera *Cystophora* (sporelings and juveniles), *Halopteris*, *Dictyota*, *Pachydictyon* and *Lobospira*. The last two genera are common in the drift (Shepherd 1973) and are probably taken as detritus.

The species of the third group, *D. odontis* and *B. squamifera*, occur on the upper sides of boulders and feed substantially on crustose corallines and the same genera of brown macroalgae listed for the previous group.

Of the fourth group, *C. limbatus* lives on the under sides of boulders and *G. imbricata* in sand or gravel under boulders. Both species graze on crustose and geniculate corallines as well as taking drift seagrass and some brown macroalgae.

The last species *S. antipodes* lives on the under sides of boulders or in fissures, where it feeds exclusively on drift macroalgae and seagrass, as do the abalone *Haliotis scalaris* and *H. laevigata* in the same habitat (Shepherd 1973).

#### Experimental Removal of Archaeogastropods

By 23 November 1983, after 65 days, a low turf of erect, filamentous algae to about 5 mm high, mostly *Polysiphonia sertularioides* had grown on the upper surfaces of the boulders in the four structures kept free of grazing molluscs. Mean biomass (d.w.) of the turf algae was 19 mg cm<sup>-2</sup> (s.e. 4 mg) and of the trapped sediment 87 mg cm<sup>-2</sup> (s.e. 4 mg). On boulders subject to natural grazing there was no algal turf and little sediment (3.7 mg cm<sup>-2</sup>, s.e. 0.6 mg). On the same date three of the turf-covered boulders from the structures were replaced among other boulders at the base of the boulder slope. When inspected on the following day a number of *D. odontis* and *B. squamifera* and their grazing trail marks were observed on the turf. By 30 November 1983 the algal turf was gone exposing the crustose layer of apparently dead crustose corallines. Ungrazed boulders in the structures were still covered by filamentous algae and sediment, and the original grazed control boulders still retained a healthy layer of crustose algae. It was concluded that in the absence of grazing molluscs filamentous algae covered upper surfaces of boulders and, with entrapped sediment, smothered the crustose algal layer.

#### Discussion

Guilds of grazing archaeogastropods have received little attention in the literature and this is the first such study for southern Australian waters. The diversity of species matches that of chitons at the same site (Kangas and Shepherd 1984) and they are similarly distributed throughout the depth range. In contrast with the chitons, however, these archaeogastropods appear to prefer a habitat free of sediment and so decline in abundance at 5m depth, where rock is buried by sand. However, the abundance of drift seagrass, epiphytes and drift macroalgae at 4 - 5m depth may account for the increased abundance at about 4m deep of those species (*M. plebejus*, *P. ventricosa* and *S. antipodes*) which feed on them.

Hawkins and Hartnoll (1983) considered that most archaeogastropods are generalist grazers feeding on whatever is available. However, Steneck and Watling (1982) suggested that the rhipidoglossan radula of archaeogastropods, with its lack of buccal strength and inherent weaknesses in tooth structure was ill-adapted to rasping leathery macrophytes or coralline algae. While the species considered in this paper have a much more varied diet than predicted by Steneck and Watling's scheme, the minor differences between their diets suggest some choice of food. Given the need for caution in inferring food preferences from gut contents, the abundance of macroalgae, corallines, crustose species and algal drift in the habitat imply that consistent differences are likely to be real ones, particularly if they coincide with micro-habitat differences between species. However, filamentous algal species, rare in the boulder habitat, may be preferred by several of the grazers, as demonstrated by the rapidity with which they were grazed from the ungrazed boulders replaced on the boulder slope.

The removal experiment suggests that archaeogastropods and chitons together control the growth of filamentous algae on the rock surface. The chitons *Chiton diaphorus* and *Chiton calliozonus* (Kangas and Shepherd 1984) and the archaeogastropods *D. odontis* and *B. squamifera* observed in this study all graze on the upper surfaces of boulders and appear to be the principal agents of such control. Sediment and algal films are known to inhibit the growth of crustose algae (Slocum 1980 and review of Hatcher 1983) and the decline of crustose corallines and *Petroderma* on ungrazed boulders is consistent with this. Thus grazing by these archaeogastropods might be expected to influence considerably the algal community structure. This can best be shown by longer term experiments.

This study and that of Kangas and Shepherd (1984) show that at least 22 species of archaeogastropods and chitons share the same boulder habitat and have strongly overlapping diets. How is this co-existence maintained? It is possible that they have partitioned their resources in subtle ways and are in stable co-existence without serious inter-specific competition (Kohn 1959, Ayal and Safriel 1982). Alternatively they may be able to tolerate a high similarity in requirements without their co-existence becoming precarious (MacArthur 1972). Another possibility, that is more easily testable, is that predators prevent the molluscan populations increasing to a level where competition for resources may occur. Studies on the effect of predation by wrasses, which are abundant in the area, and known to feed on these molluscs would be valuable.



## ACKNOWLEDGEMENTS

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TABLE 1

Table 1 Species of grazing gastropods on the boulder slope at West Island, with depth range, mean density, mean size and size range, and number of gut contents analysed. In each case the length measurement is columellar length.

Species	Depth (m)	Mean Density (Nos. m <sup>-2</sup> )	Length (mm) Range	Number Used	
				Mean in Feeding	Study
<i>Scutus antipodis</i> (Montfort)	4-5	2.9	38-90	61.1	8
<i>Clanculus (Euriclanculus) limbatus</i> (Qoy and Gaimard)	1-5	10.2	13-21	19.1	10
<i>Clanculus (Mesoclanculus) plebejus</i> (Philippi)	0.5-5	44.6	6-8	7.3	10
<i>Diloma (Chlorodiloma) odontis</i> (Wood)	0.5-5	5.5	16-22	18.8	10
<i>Gibbula (Notogibbula) preissiana</i> (Philippi)	1-5	12.7	7-8	7.8	10
<i>Granata imbricata</i> (Lamarck)	1-5	6.2	24-35	28.2	10
<i>Euchelus aspersus</i> (Philippi)	1-4	2.3	7-10	8.7	10
<i>Turbo (Subnivalia) undulatus</i> (Solander)	0.5-5	9.8	26-40	33.8	10
<i>Turbo (Nivalia) torquatus</i> (Gmelin)	1-4	1.1	28-74	43.0	8
<i>Bellastraea squamifera</i> (Koch)	3-5	5.7	13-15	14.3	10
<i>Phasianella ventricosa</i> (Swainson)	2-5	12.9	8-14	28.2	10
Rare species not used in feeding study					
<i>Cantharidus (Phasianotrochus) eximius</i> (Perry)	3	< 0.1	18-25	21.5	-
<i>Thalotia (Prothalotia) lehmanni</i> (Menke)	3-5	< 0.1	16-20	18.0	-
<i>Thalotia (Prothalotia) pulcherrima</i> (Wood)	3-5	< 0.1	13-18	15.5	-
<i>Clanculus (Macroclanculus) undatus</i> (Lamarck)	1-4	< 0.1	24-30	27.0	-
<i>Clanculus (Mesoclanculus) consobrinus</i> (Tate)	2-5	< 0.1	14-15	14.5	-
<i>Stomatella auricula</i> (Lamarck)	4-5	< 0.1	10-14	12.0	-

- Fig 1. Map of West I. showing the algal communities of the boulder slope in Abalone Cove. The granite blocks shown are prominent topographic features bearing similar algal communities to surrounding boulders.
- Fig 2. Distribution with depth of density of archaeogastropods on the upper (hatched) and lower (blank) sides of boulders.
- Fig 3. Distribution with depth of density of *G. preissiana* and *D. odontis* in March (continuous line) and September (dashed line) 1983.
- Fig 4. Mean percentage composition of food categories in the gut of 11 species of archaeogastropod grouped according to affinities in diet (see Fig. 5).
- Fig 5. Dendrogram showing affinities in diet between 11 species of archaeogastropod.

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Fig. 1

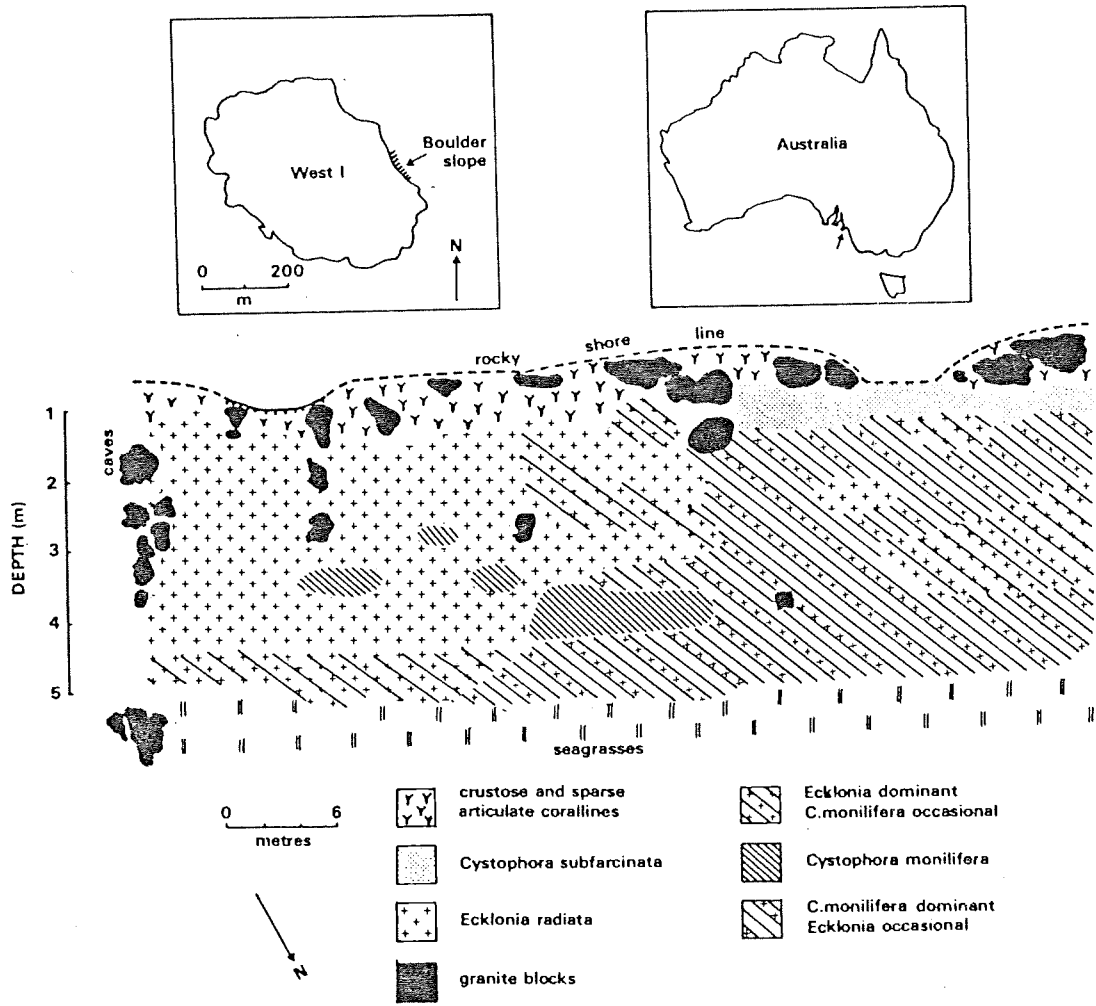
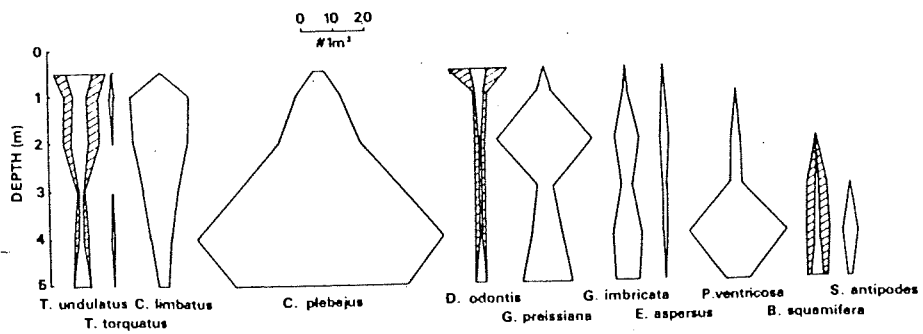


Fig. 2



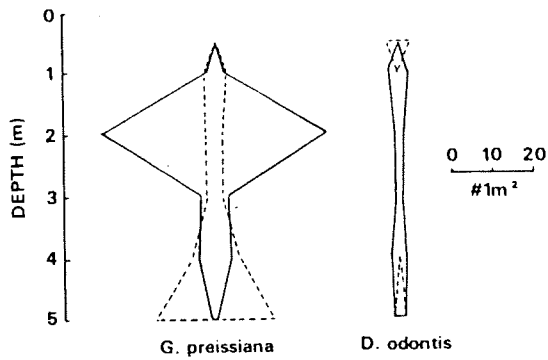


Fig. 3

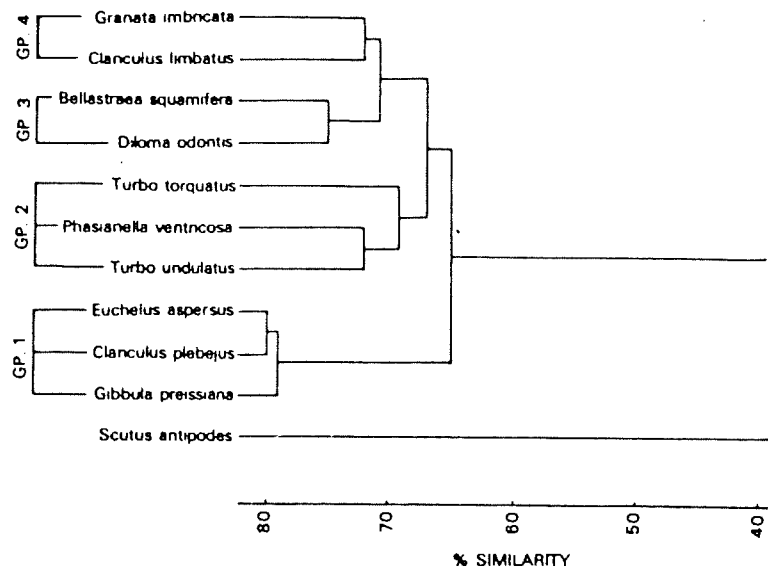


Fig. 5

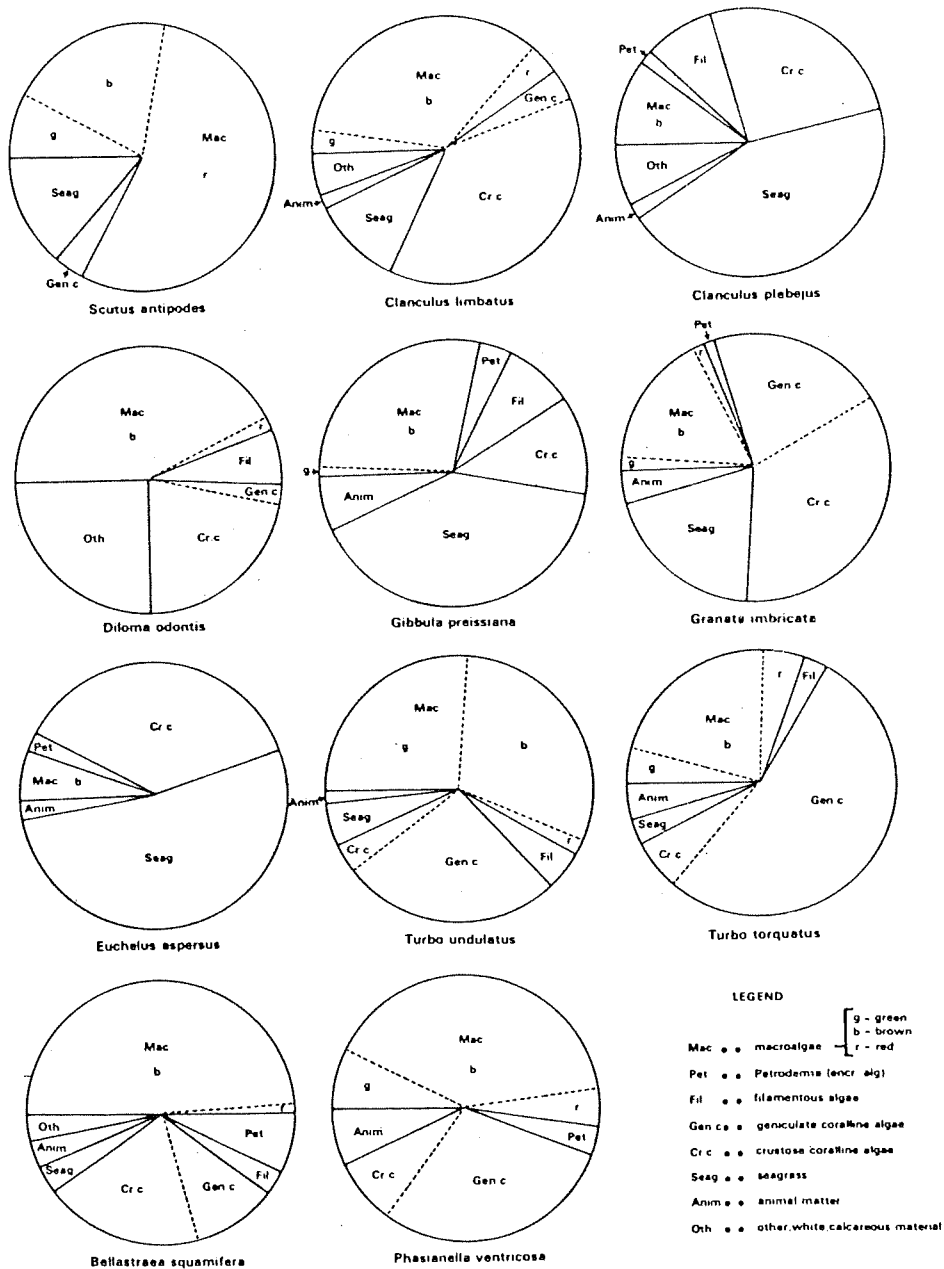


Fig. 4

APPENDIX 6

Extract of paper on feeding of the blue-throated wrasse, and  
abalone size preferences by different size classes of wrasse.  
(ms in preparation).

On the social behaviour and feeding of the  
Blue-Throated Wrasse Pseudolabrus tetricus

by S.A. Shepherd and P.S. Clarksont

ABSTRACT

The blue throated wrasse Pseudolabrus tetricus is a protogynous species living in shallow rocky reef areas in permanent harem groups of females dominated by a few large monandric males. The harem groups occupy home ranges attached to particular shelter holes.

Sexual maturity occurs at 20-22 cm length at age 2, and sex inversion at about 35 cm length at age 5 or more.

The species is carnivorous and its diet changes with increasing size. Small individuals feed on amphipods, micro-molluscs and animals living in algal turf, and large individuals on shrimps, crabs and larger molluscs.

Foraging is restricted to daylight hours and reaches a peak in the morning, and declines around afternoon and dusk. Agonism within and between species is low. It is suggested that the species' requirement for shelter and the patchy distribution of its food has influenced the evolution of its social system.

## Food Eaten

The diet of P. tetricus changes with increasing size (Fig. 7). Small individuals eat mostly amphipods, micro-molluscs and ophiuroids which live in the algal turf or among macro-algae. The shrimp, crab and molluscan components of the diet increase with increasing fish size. The composition by species (or highest category identified) of the various components of the diet for 4 size classes of fish (Table 4) gives more information on the changes of diet within prey taxonomic groups. Among the molluscs the species composition changes from micro-molluscs (e.g. Notosetia) to larger species (e.g. Phasianella, Thalotia and Conus). Among the crustaceans shrimps and snapping prawns are replaced by crabs.

The change in gastropod prey size with increasing predator size is shown by a graph of maximum length of gastropod eaten against size class of fish (Fig. 8).

In addition we evaluated experimentally the size selection for abalone (mostly H. scalaris) by different sizes of P. tetricus. During field studies of abalone we overturned boulders, measured the size of abalone under them and allowed P. tetricus to search the boulder for prey abalone.

Observations on the size of abalone taken, not taken, and unsuccessfully attacked (Fig. 9) show that larger fish take more abalone and that the size range of abalone taken also changes. The numbers of abalone taken by fish 20 - 25 cm long were significantly less than the number taken by either fish 25 - 30 cm long (Fisher exact test:  $P = 0.006$ ) or fish 30 - 35 cm long (Fisher exact test:  $P = 0.03$ ). Although there was no significant difference between the total numbers taken by fish 25 - 30 cm and 30 - 35 cm long respectively, a comparison of the number of abalone < 15 mm long taken by each size class of fish, showed that substantially fewer were taken by fish 25 - 30 cm long than by fish 30 - 35 cm long (Fisher exact test:  $P = 0.06$ ).

Percentage Composition by Species (or higher taxonomic category) of Echinoderm, Molluscan and Crustacean components of the diet of *P. tetricus* in different size classes.

Species/Taxonomic Group	Fish Length Class (cm)			
	10-20	20-30	30-40	40+
<u>ECHINODERMS</u>				
<u>Echinoids -</u>				
<i>Heliocidaris erythrogramm</i>	-	-	4.4	2.2
Temnopleuroid urchins (mostly <i>Holopneustes</i> and <i>Amblypneustes</i> )	-	4.0	1.7	-
<i>Coscinasterias calamaria</i>	-	3.5	0.8	-
<u>Ophiuroids</u>	7.0	-	0.7	-
<u>MOLLUSCS</u>				
<u>Chitons</u>				
<i>Chiton diaphorus</i>	0.6	-	-	-
<i>Cryptoplax striata</i> (Lamarck)	-	-	0.6	-
<i>Ischnochiton australis</i> (Sowerby)	-	3.1	2.7	7.3
<i>Ischnochiton contractus</i> Reeve	-	1.9	1.0	-
<i>Notoplax speciosa</i> (H. Adams)	-	0.5	-	-
Unidentified chitons	-	0.5	0.6	0.1
<u>Gastropods</u>				
<i>Clanculus limbatus</i> )	0.7	-	8.2	-
<i>Clanculus plebejus</i> )				
<i>Cominella lineolata</i>	1.1	-	-	-
<i>Conus anemone</i>	-	-	1.6	2.8
<i>Cypraea comptoni</i>	-	-	0.5	-
<i>Diloma odontis</i>	-	1.4	0.6	1.6
Fam Fissurellidae	-	0.3	2.6	-
<i>Gibbula preissiana</i>	-	0.7	-	0.4
<i>Haliotis spp.</i>	-	3.3	0.3	-
<i>Littorina sp.</i>	0.2	-	-	-
<i>Lyria mitraeformis</i>	-	-	-	0.4
Fam. Mitridae ( <i>Mitrella spp.</i> )	-	5.0	2.4	-
<i>Nassarius sp.</i>	-	-	0.5	0.4
<i>Nerita sp.</i>	1.7	-	-	-
Fam. Rissoidae (mostly <i>Notosetia sp</i> )	9.7	-	-	-
Super Fam. Patellacea (limpets)	3.6	1.5	2.1	-
<i>Pleuroploca australasia</i>	-	-	-	2.5
<i>Phasianella ventricosa</i>	-	2.2	8.0	18.1
<i>Pyrene sp</i>	-	0.5	-	-
<i>Stomatella auricula</i>	-	0.5	-	-
<i>Thalotia lehmanni</i>	-	2.8	10.9	8.1
<i>Turbo undulatus</i>	-	0.2	-	-



Species/Taxonomic Group	Fish Length Class (cm)			
	10-20	20-30	30-40	40+
<u>Bivalves</u>				
Fam. Mytilidae (mussels)	2.2	2.8	2.3	1.5
Fam. Pectinidae (scallops)	-	2.8	3.5	4.2
Unidentified bivalves	2.4	3.7	2.1	0.3
<u>CRUSTACEANS</u>				
Decapod				
Crabs (mostly <i>Plagusia chabrus</i> )	-	6.5	18.4	18.8
Others	0.7	3.4	4.0	0.4
Fam. Paguridae (hermit crabs)	-	2.5	10.5	26.3
Fam. Palaemonidae (shrimps)	3.9	19.2	2.8	4.6
Fam. Synalpheidae (snapping prawns)				
Other Shrimps	-	-	1.6	-
<u>ASCIDIANS</u>	-	-	0.7	-

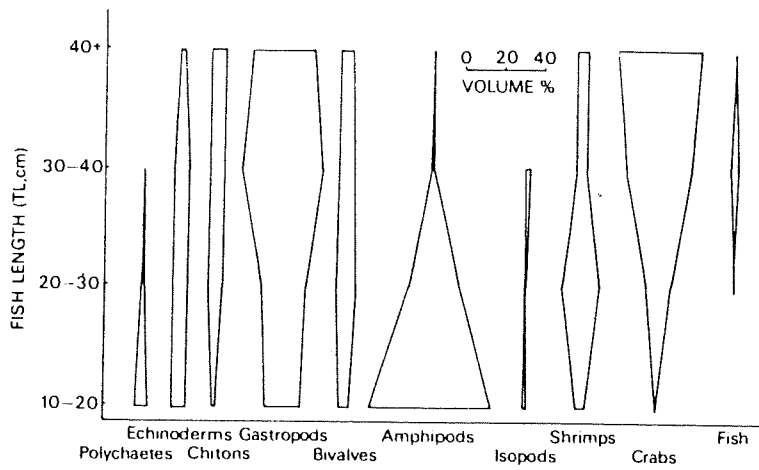


Fig. 7

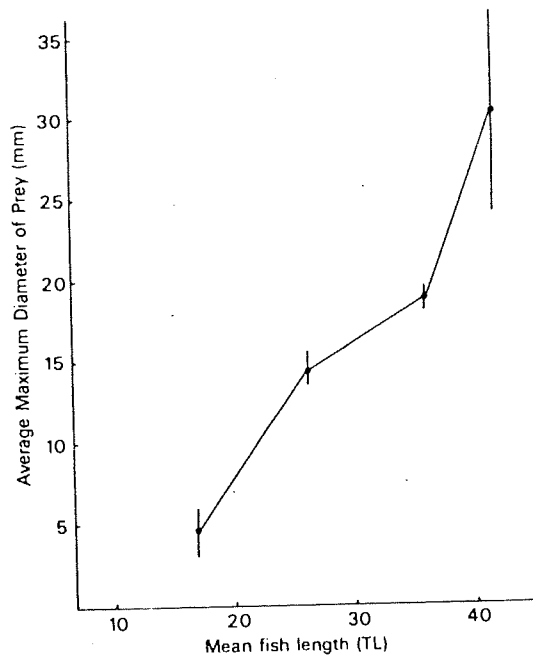


Fig. 8

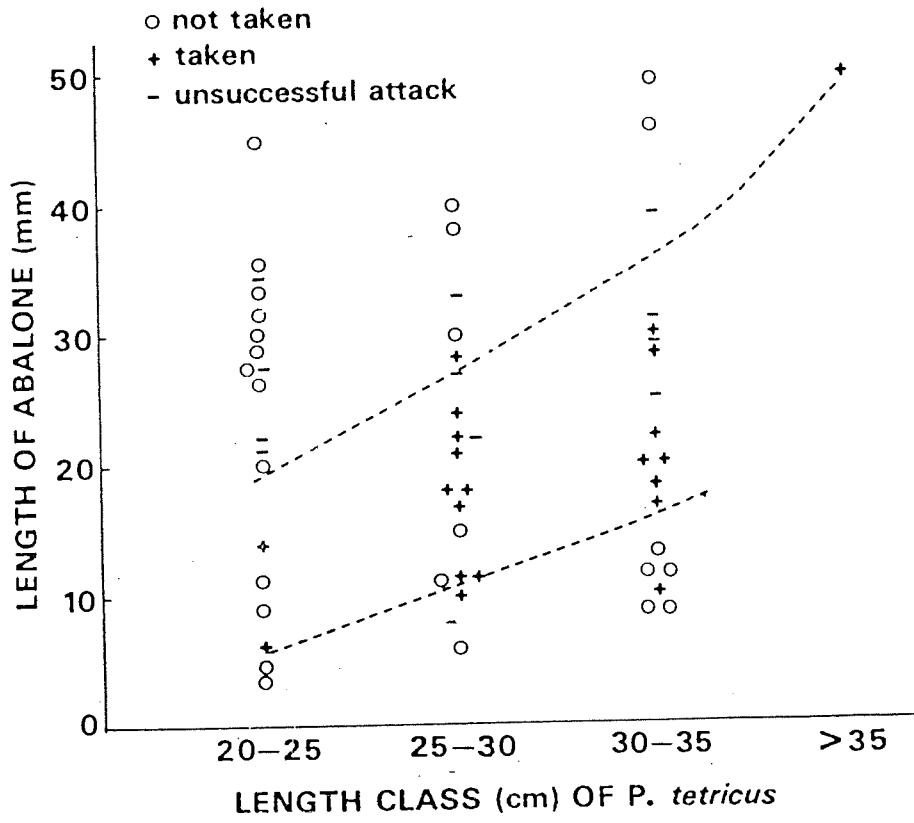


Fig. 9

APPENDIX 7

Recruitment and mortality of H. laevigata over  
14 years with notes on predators of adults.  
(ms submitted to AJMFR).

STUDIES ON SOUTHERN AUSTRALIAN ABALONE (GENUS Haliotis)

VI\* RECRUITMENT AND MORTALITY OF H. laevigata OVER 14 YEARS  
WITH NOTES ON PREDATORS OF ADULTS.

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RUNNING TITLE: RECRUITMENT AND MORTALITY OF H. laevigata

key words: Abalone, Haliotis, marine molluscs, recruitment,  
mortality, population dynamics, predators,  
predator-prey interactions, density-dependent  
mortality, shell production.

\* Part V, Trans R. Soc. S. Aust., 1985,

## ABSTRACT

The recruitment strength and natural mortality of a population of the abalone Haliotis laevigata Donovan at West Island, South Australia, was measured from 1970 to 1984. Recruitment varies widely from year to year, but pulses of good recruitment tend to occur in summers with above average sea temperatures.

Recruitment is positively correlated with the mean summer sea temperature anomalies but two exceptional years have obscured the relationship. No evidence was found that spawning stock size is a significant variable contributing to recruitment variability.

Natural mortality rates ranged from -0.01 (s.e. 0.12) to 1.1 (s.e. 0.03) over the same period with a long term oscillatory trend, and showed delayed density dependence.

Dead shell collections from the study site show that stingrays cause up to 88% of the total mortality of abalone 3 years and older, and octopuses, crabs and others the remainder.

## INTRODUCTION

Although recruitment and mortality are the principal mechanisms regulating the size of natural populations of animals, they are difficult to measure and hence are poorly understood among marine invertebrates and molluscs in particular. A knowledge of these mechanisms, and of the factors influencing them, is essential to establish guidelines for the management of exploited species.

Studies to measure these parameters have usually been over a relatively

short time so that environmental and density dependent effects (the latter often assumed) (Hancock 1973, Shepherd and Cushing 1981) have rarely been confirmed.

Recruitment is usually sporadic or fluctuates widely among molluscs, such as oysters (Korringa 1962), scallops (Olsen 1955), cockles (Hancock 1973), razor fish (Butler and Keough 1981) and whelks (Phillips 1969), and evidence of any relationship between density of adults and numbers of recruits is still lacking (Spight 1975; Underwood 1979). However, the influence of oceanographic conditions, such as sea temperature on recruitment has been demonstrated for some temperate fishes (Shuntov et al. 1980) a scallop (Caddy 1979) and suggested for Haliotis tuberculata L. (Forster et al. 1982).

The greenlip abalone, Haliotis laevigata Donovan is a sedentary species occurring along the southern Australian coast in disjunct populations which are exploited commercially mostly between 134° and 139° east longitude (Shepherd 1973). Spawning occurs from spring to autumn (Shepherd and Laws 1974) and the lecithotrophic larvae settle after a few days, on crustose corallines in crevices in the same general area as adults (Shepherd 1973, Shepherd and Turner 1985). Juveniles remain cryptic and are difficult to find until they reach a length of 50-70 mm, when they begin to emerge from crevices into a more open habitat where they become accessible to a diver.

A population of H. laevigata occurs in Abalone Cove on the lee of West (35°36'25"S., 138°35'27"E.) and in very low densities at the edge of a submerged reef between the Island and King Head (Fig. 1). The nearest other known populations of H. laevigata are 10 km east and about 15 km west.

The study site extends for 80 m along the shore at the base of a boulder slope within the West I. marine reserve, and all abalone are protected from exploitation. This paper describes fluctuations in recruitment, mortality and population size of H. laevisgata at the study site from 1970 to 1984 and explores the factors influencing mortality and recruitment. Dead shell collections from 1982 to 1984 enabled an assessment of the agents of mortality in those years. In this paper the term recruitment is used to mean the process in which the young abalone first become accessible to the research diver at an age of 1<sup>1</sup>/<sub>2</sub> - 2 years.

## MATERIALS AND METHODS

### Field Measurements

Counts of H. laevisgata at the study site have been made by the author at intervals of 2 to 5 months (with a few longer gaps) since 1970. The diver moved carefully over the whole area and measured all accessible individuals. Before 1978 measurements were made with a vernier caliper, and the data written on a slate, but after that the diver used a gauge which impressed on a plastic strip each datum on length (Fig. 2). The use of the gauge reduced the time underwater for each census from about three hours to two.

Distributional data for H. laevisgata for Fleurieu Peninsula were obtained from interviews with the professional abalone divers allotted to the zone and numerous other divers familiar with the coast. A number of spot and sled divers have also been made by the author. Densities of H. laevisgata between West Island and King Head were obtained in a survey in 1983.

### Shell Production

In December 1981 all accumulated shells and shell fragments of H. laevisgata were removed from the study site and thereafter until December 1984 at



about bi-monthly intervals, deposits of fresh shell and fragments were collected. 'Old' shell characterised by a dull inner surface and often encrustations were occasionally exposed above the sand and were removed but not included in the counts.

Shells were measured and examined for breakage patterns. Only those parts of shells with a body whorl were included, for determination of shell production; their length was estimated in 10 mm size classes by reference to a standard set of shells. Shells were classified as (1) unbroken, (2) with chipped edges and (3) broken.

The potential shell production of individuals  $\geq 90$  mm (i.e. 3 years old) was estimated by subtracting the number of individuals alive at the end of the year from those alive at the beginning (derived from the census data and the calculated mortality rate) and dividing the result by the censusing efficiency (E) of the diver (i.e. the proportion of the total numbers seen by the diver). E was determined from 5 replicate censuses of the site, by dividing the number seen by the diver in a normal census by the number seen by two divers together systematically and exhaustively censusing the same area. The replicates were done at different times of the year and in different swell conditions. The mean value of E was 0.77 (s.e. 0.02).

#### Environmental Data

Sea temperatures to 0.1°C have been recorded at about 8 a.m. at 0.5m depth on most visits to West I. since 1965. Early data to 1969 are summarised by Shepherd and Womersley (1970). A curve of mean sea surface temperatures (SST) for the summer period from November - February for West I. was obtained by regression analysis and the mean variation of

summer records from the mean curve obtained for each summer from 1966 - 1984 except for the summers of 1977 and 1979 for which data were lacking.

Mean monthly maximum summer (November - February) air temperature (A.T.) were obtained for Victor Harbor (2 km distant from West I.) from the Bureau of Meteorology and the annual mean summer monthly variation from the long term mean determined for 1966 - 1984. Mean summer (December, January) ocean surface temperatures are available from 1974 from the permanent oceanographic station off Cape Northumberland (38°10'S.; 140°4'E.) (Lewis 1981). The monthly summer variation in ocean temperature (O.T.) was determined for 1974 - 1984.

SSTs at West I. were weakly correlated with Victor Harbor A.T. ( $r=0.52; P<0.05$ ) but a strong correlation resulted from the inclusion of O.T.s in the regression ( $R^2=0.89; P<0.01$ ). From the derived equation

$$\text{SST (West I.)} = -0.34 + 0.91 \text{ O.T.} + 0.68 \text{ A.T.}$$

estimates of mean summer variation of SST at West I. were obtained for 1977 and 1979.

#### Analysis of length-frequency distributions

Due to incomplete recruitment of younger year-classes (see below), length-frequency distributions lack the 0+ year-class and are under-represented in the 1+ and 2+ classes; the older year-classes tend to coalesce to form a single mode, although the 3+ year-class is sometimes identifiable (Shepherd and Hearn 1983).

Hasselblad's (1966) method incorporated in the NORMSEP computer program (Abramson 1971) was used to separate year classes. The procedure assumes that the distribution is composed of Gaussian component distributions which are separated by maximum likelihood methods. The method requires a

degree of subjectivity when choosing upper and lower boundaries for modes, but the fitting is aided by using the average annual growth increment as a guide. In no case did the algorithm converge on the chosen boundaries. The programme separated and computed numbers in the 1+, 2+ (and sometimes 3+) year-classes and combined the remainder. P values  $>0.05$  (Table 1) indicate statistically satisfactory fits. In the few cases (see Table 1) where the program failed to separate the 1+ and 2+ year classes, Hancock's (1965) method, which partitions the size distribution into approximate year classes by a knife edge separation based on the average growth increment, was used.

#### Recruitment

In this study a mean birthdate for H. laevigata is fixed at 1 January (Shepherd and Laws 1974, Shepherd and Hearn 1983). The strength of recruitment is difficult to measure for this species because of its cryptic behaviour when young (Shepherd 1973). Plots of the numbers in each annual 1+ age class show that numbers are at first very low but increase markedly at 16-18 months presumably as individuals emerge from the under-boulder habitat. Because the process of recruitment is gradual and might vary from year to year due to a seasonally variable larval settlement the estimate of recruitment adopted was the mean number of individuals in a cohort between 16 and 24 months old.

### Mortality

The instantaneous mortality rate, M, was calculated only for individuals 3 years and older, because younger individuals were still partly cryptic. The natural logarithm of numbers, N, of these year classes combined were regressed against time, t, to give a slope of -M (Gulland 1969, p. 64).

For example, for 1973, the data used were:

	26.xii.72	29.v.73v	6.x.73	17.ii.73
Cumulative No. of days	1	154	284	356
Numbers	232	166	119	113

Note that the first datum (232) includes individuals in the 2+ year class.

Estimates of M with standard errors were calculated for approximate calendar yearly periods (Table 2) using the data in Table 1. Assumptions of the method are that mortality is independent of age and constant over the chosen time interval. The former condition is met by this species (Shepherd et al. 1982) and seasonal variations in mortality appear to be minor (see below) and unlikely to introduce serious error.

### Biomass

The biomass of individuals in different size classes was calculated by converting numbers in each length class (from length-frequency data) to weight by using the equation derived for H laevigata at West I.

$$W = 0.045 L^{3.41} \quad (N = 34; \quad r^2 = 0.95)$$

where W = total weight in g and L = shell length in cm. The population size in 1976 was not known directly, but was extrapolated from the 1977

census by using the mean mortality rate calculated for the period 10.vi.75 - 21.ix.77.

## RESULTS

The numbers of H. laevigata in each year-class or group of year-classes for each census from December 1970 to December 1984 at the study site are given in Table 1. Changes in the total population, biomass of effective spawners (i.e. individuals > 120 mm long), numbers of individuals in successive annual cohorts, from the age of one to three years, and annual mortality rates are shown in Fig. 3. Numbers in the 'total' (i.e. censused) population were low in 1970 (and during 1969 - unpublished observations) but increased sharply from 1971 to 1975. This was due to strong recruitments in 1972 and 1973 and to an increase in number of older individuals in 1971 and 1972, presumably from a strong recruitment in 1968 (see below). Numbers declined from 1975 until December 1979 due to high mortality rates for much of the period, and then increased until 1981 as adult numbers increased. After a brief decline in 1981 numbers increased again until March 1983 when they declined again with the effect of high mortality in 1983 and 1984. The strong recruitments of 1972 and 1973 would have been reflected in an increase in number of adults 5 years later in 1977 and 1978 had not poachers taken them in 1977 (see note to Table 2).

In the following section recruitment and mortality patterns over time are examined in relation to environmental and other factors.

### Recruitment

Factors which may influence annual recruitment strength include total egg

production and sea temperature. Because the number of eggs produced by a female abalone > 3 years of age is linearly related to its weight (unpublished data) the mid-summer biomass of an adult abalone population is a good index of total egg production. It is assumed here that all eggs are spawned i.e. no resorption occurs. Studies on reproduction of this species over several spawnings (Shepherd and Laws 1974) and in 1983 and 1984 (unpublished data) have always shown a uniform decline of the size of the gonad during the spawning season with no histological evidence of resorption of unspawned eggs. The parent stock responsible for the recruitment of H. laevigata at West Island is unknown. However, the total catch of H. laevigata taken by professional divers for the period 1971 - 1983 in southern Fleurieu Peninsula (see Fig. 1) is significantly correlated ( $r=0.67; p<0.05$ ) with the biomass of adults (>120 mm long) at the study site. During this period fishing effort was stable so that the total annual catch can be considered to reflect stock abundance for the region. Thus the adult biomass at West I. may be considered a crude index of egg production in the area during the period under consideration.

Variations of mean SSTs at West I., of mean maximum A.T.s at Victor Harbor and of O.T.s from long term means are shown in Fig. 4.

Except for 1968, 1973 and 1981-3 sea and air temperatures at West I. have been below long term means. Ocean temperatures since 1974 show mainly alternating cool and warm summers. It is apparent, and was confirmed by the regression (see methods), that SST anomalies at West I. are a combined effect of local solar heating and background O.T. anomalies.

A plot of recruitment against SST anomalies at West I. for 1969-1984 (Fig. 5) shows a trend of high recruitment at higher sea temperatures. However, the correlation for 16 years of data is significant only at the 10% level ( $r = 0.43$ ). Anomalous years were 1972 and 1983. Exclusion of the 1972 data resulted in a significant correlation ( $r = 0.55$   $P < 0.05$ ). Recruitment in 1983 proved to be poor, in spite of an apparently strong settlement in that summer (Shepherd and Turner 1985). Evidently pre-recruitment mortality was high, although whether it was exceptionally high is not yet known.

Multiple regression analyses including spawning stock size as a variable were attempted but the latter proved non significant in every case. However a relationship was found between recruitment and spawning stock size (those  $\geq 120$  mm only<sup>+</sup>, corresponding to 5 year olds and above) and the square of sea temperature anomalies by multiple regression analysis.

The results of the analysis for the years 1970-84 (Table 4) give significant terms for both variables only after exclusion of the 1972 data.

#### Mortality

Instantaneous mortality rates and their standard errors for approximate annual periods are given in Table 2 for 1970 - 1984 and calendar yearly values are plotted in Fig. 3.

These mortality rates were compared with those obtained from the analysis

#### Footnote

<sup>+</sup>The other size classes were removed from the regression equation as indicated by a partial F test.

of sightings of marked individuals for two overlapping periods (Table 3) from Shepherd et al. (1982). The two data sets are independent because marked individuals were taken from outside the study site and were not included in the censuses. Although the estimates cannot be compared by formal statistics the overlap of standard errors indicate there is no significant difference between them. There is the obvious caveat, however, that estimates with wide standard errors and those for the years when there were few censuses (e.g. 1975-77) should be accepted with caution.

Lag correlations between annual mortality rates and population size were sought for mean annual numbers of (a) 2 year old individuals and older, and (b) 3 year olds and older. These cumulative age classes were selected for comparison because a major predator of this abalone species, the stingray (see below), takes some 2 year olds, but a majority of 3 year olds and older. A plot of correlation coefficients for various lag time periods (Fig. 6) shows values significant at the 5% level only for those 2 year old and older with a lag period of 12 months, but a value significant at the 10% level for those 3 years old and older with a lag period of 6 months.

#### Dead shell production

A total of 348 shells, excluding old ones, was removed from the study site over the 3 year period 1982 to 1984. The number of shells in 3 categories of shell for each year is given in Table 5. Broken shells accounted for 69% of the total, unbroken shells 23% and those with chipped edges 8%. The size distribution of shells in these categories is shown in Fig. 7. Broken shells are mostly in the length range 100-150 mm and are the result of stingray Dasyatis brevicaudata (Hutton) and Myliobatis australis (Macleay) attack (Shepherd 1973). It is common for shells to



be broken into many fragments by these rays and in two observed attacks the ray swam off with the abalone. Hence some loss of shells from the area through stingray attack must occur.

The causes of mortality resulting in intact shells are uncertain. The sea-star Coscinasterias calamaria (Gray) leaves undamaged shells, but it is rare at West I. and predation by it on H. laevigata has never been observed there.

The octopus, Octopus flindersi (Cotton) is a known predator (Shepherd 1973), but it does not appear to drill a hole, as is typical of other octopus species (personal observations of attacks, and see Pilson and Taylor (1961), Ambrose and Nelson (1983)). Hence the occurrence of intact shell, although probably a result of its predation, cannot be unambiguously attributed to it.

Shells with chipped edges are mostly in the length range 40-80 mm and may result from crab (species are listed in Shepherd 1973) predation. Similar damage from crabs is reported by Cox (1962), Kojima (1981) and M.J. Tegner (pers. comm.) but questioned by Hines and Pearse (1982) who consider that wave action and abrasion are more likely causes of this kind of damage.

Shells < 50 mm length are poorly represented in the collection of shells. This is because major predators of this size group are wrasses (Shepherd and Turner 1985) which crush and ingest the shell.

In order to estimate fully the extent of predation by stingrays on this abalone, the number of shells lost from the study site must be obtained. It is assumed that this loss is due to stingray attack. Table 6 gives

the potential shell production at the site (see Methods), the actual numbers of shells found and by subtraction the number of shells lost. These are then added to the numbers of broken shell found to give an estimate of numbers taken by stingrays. Thus, for 1983, 88%, and for 1984 87%, of the total mortality of individuals  $\geq 3$  years old was estimated to be due to stingray attack. Predation by stingrays on younger individuals (i.e.  $< c. 90$  mm) (Fig. 7) adds another few percent to this total. The size distribution of dead shells (Fig. 7) for 1982-4 differs significantly from the size distribution of live shells, obtained by averaging all censuses taken during the same period (Kolmogorov - Smirnov test comparing the two distributions -  $D = 0.33; P < 0.01$ ), suggesting that mortality is relatively more intense on larger than on smaller abalone. However, an assumption of this conclusion is that differential loss of shells between size classes does not occur.

The actual annual shell production ratios for 1982 to 1984 (i.e. 27:89:168) do not differ significantly from the potential annual shell production ratios (see Table 6) for those years ( $\chi^2$  goodness of fit test:  $\chi^2 = 4.01$  n.s.). Thus shell production values are consistent with the trend in mortality rates independently derived for those years.

Hines and Pearse (1982) used annual shell production figures to estimate the natural mortality of abalone. For this to be possible for species like H. laevigata where loss of dead shell occurs, it would be necessary to estimate independently that loss.

#### Sighting of predators

All sightings of stingrays (with estimates of their size) and octopuses during dives were recorded from January 1982 to December 1984. Stingrays

were known to rest in certain caves near the study site and these were inspected on each dive.

Octopuses did not occupy specific caves or middens and sightings were chance encounters. The number of sightings of these predators (Fig. 8) were few in 1982 but increased substantially in 1983 and 1984.

A plot of the estimated number of abalone taken each year (see Table 6) by stingrays against the cumulative annual number of sightings of stingrays, and of numbers of intact shells against number of octopuses seen for 1982- 1984 (Fig. 7) shows in each case a trend of increasing numbers taken with more sightings, and suggests that sightings are a measure of the incidence of predation. The probability of the observed trends for both predators occurring by chance is 1/36 or substantially less than 0.05.

## DISCUSSION

### Recruitment

Variability in recruitment is common among many marine invertebrates (Hancock 1973) and the few long term studies on abalone populations suggest this is also true for them.

Forster et al. (1982) monitored the population size of Haliotis tuberculata L. from 1968-1980 and found a marked long term decline in numbers. They related this and earlier historic declines to summer sea temperature anomalies affecting recruitment. Kojima et al. (1978) observed fluctuations of 6 to 12 year intervals in the catch of Haliotis discus discus Reeve over 70 years. Sainsbury (1982 a,b) found heavily skewed length frequency distributions of Haliotis iris Martyn and suggested that population size fluctuations occurred because a sporadic good recruitment was followed by

long periods of poor recruitment. Conversely Hines and Pearse (1982) reported stable populations of Haliotis rufescens Swainson and H. walallensis Stearns from 1972-1981 with constant mortality and recruitment rates.

H. laevigata has shown periodic strong pulses in recruitment at West I. and these appear to have contributed to the basic oscillatory trend in the population size. However it is not yet known whether these pulses represent strong larval settlements or changes in pre-recruit mortality. The tendency for recruitment pulses to occur in summers with above average sea temperatures suggests that it is larval settlement that is temperature dependent but this is conjectural in the absence of knowledge of the agents of pre-recruit mortality. Variability in larval settlement from year to year does occur, because Shepherd and Turner (1985) found large differences between early post-settlement densities of H. laevigata between 1983 and 1984.

The correlation between recruitment and sea temperature anomalies may have direct or indirect causes. Larval development rate among haliotids is temperature dependent. For example Leighton (1974) and Leighton et al. (1981) found that the swimming larval phase for Haliotis fulgens Philippi is reduced from 9 days at 16°C, 5 days at 20°C to 3.5 days at 24°C. D.N. Morrison (pers. comm.) found that the swimming time of H. laevigata larvae was less than 2 days, but temperature data were not kept. With such abbreviated swimming time larval dispersion may be only a few km at West I. where the maximum tidal excursion is about 5 km (unpublished data). Slight temperature differences could substantially prolong or shorten

larval life and hence affect dispersal. Alternatively, sea temperatures may reflect other critical oceanographic conditions which have a primary effect on larval dispersal. The data of Shepherd and Turner (1985) suggest that a temporal sequence of several settlement waves occurs during a spawning season. Until the conditions under which these occur are known the factors influencing settlement strength are still a mystery.

The role of adult spawning biomass (used to measure egg production) as a factor influencing recruitment strength remains problematic, and gives little hint of the nature of the underlying parent-progeny relationship that must exist. The most likely explanation of the correlation with recruitment strength is that fluctuations in biomass are a result, not a cause, of periodic recruitment pulses.

Such pulses in 1968 (a year with high SSTs), 1972-3, and 1977 would have caused spawning population peaks some 5 years later in 1972, 1977 (taken by poachers) and 1982. The approximate 5 year periodicity of these pulses, as well as of sea temperature extremes, in phase with the 10 year oscillation of mortality rates could have caused the significance of the term spawning biomass in the regression. If so, the relationship is a statistical artifact without biologic significance (Royama 1981).

#### Mortality

Adult mortality rates at the study site have shown a long term oscillation and an apparent density dependence since 1970. The rates observed have shown far greater variation than has previously been reported for abalone species, but few studies have been conducted for an extended period of time. High mortality rates are given for abalone species by Tutschulte

(1976), Doi et al. (1977) Van Sickle (1977) and Hines and Pearse (1982) and low rates (up to 0.25) by Beinssen and Powell (1979), Breen (1980) and Sainsbury (1982a). Variability in mortality rates may be more widespread than has previously been supposed.

The dead shell collection data suggest that mortality is biased toward the larger size classes, possibly because large shells are weakened by boring sponge (Cliona) attack (Shepherd 1973), whereas Shepherd et al. (1982) found no significant age dependence. Further studies on mortality in the first 3 years of life are necessary to elucidate this problem and especially that of pre-recruit mortality.

The correlations between predator sightings, dead shell production and the changing mortality rates for 1982-4 suggest that the number of predators at the site change in response to prey (abalone) density. Stingrays are the major predator, but can only take individuals resting wholly or partly in the open. They do not have access to the crevice refuge where a few large, but mostly smaller abalone occur (Shepherd 1973). At high population densities more abalone would be vulnerable to predation by rays. An increase in hunting success rate at higher abalone densities may induce stingrays to take proportionately more abalone or may induce more stingrays to remain in the vicinity (see review by Curio 1976). In either case predator behaviour is a sufficient explanation of the density dependent mortality and presumably also of any lag period involved. Both aspects need further study.

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TABLE 1

Estimates of year class strengths for *H. laevigata* during periodic censuses at West I. from 1970-1984. P = probability value. The absence of a P value indicates that numbers in year classes were obtained by Hancock's method (see text).

Age (yrs)	1970			1971			1972				
	4.xii	1.xii	7.iv	2.vii	1.x	1.xii.	25.i.	14.iv.	11.vii.	3.x	26.xii
1	20	33	53	74	64	45	0	19	22	45	50
2	31	29	49	62	60	57	76	70	63	52	68
3	}67	}63	}93	}77	33	}92	}177	}195	169	169	164
> 4					45						
Total	118	125	195	213	200	194	253	284	254	266	282
P	-	0.02	-	0.07	-	0.28	-	0.37	0.14	0.53	0.96

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Age (yrs)	1973				1974			1975		1977
	29.v	6.x	17.xii	10.iv	29.v	3.ix	23.xii	10.vi	21.ix	
1	207	193	163	47	85	188	146	67	48	
2	39	61	58	196	135	148	93	251	82	
3	52	54	51	46	}126	99	27	156	74	
> 4	114	65	62	71		46	28	76	149	
Total	412	373	334	360	346	481	294	550	353	
P	0.51	-	0.40	0.46	0.04	0.13	0.08	0.11	0.09	

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Age (yrs)	1978		1979		1980			1981		
	27.v	7.ii	24.viii	19.xii	13.vi	8.vii	13.ii	19.v	5.viii	2.x
1	103	5	27	32	93	88	15	118	56	31
2	101	45	46	27	65	43	52	61	72	40
3	91	74	142	}159	167	31	99	74	}184	37
> 4	75	121	67		167	195	113	128		118
Total	350	245	282	218	325	357	279	381	312	226
P	-	0.22	0.45	0.29	0.89	0.88	0.63	0.14	0.88	0.30

Table 1 (contd)

	1981		1982			1983			
	9.xii	6.ii	22.v	13.x	14.xii	2.iii.	18.v.	23.viii	12.xii
1	55	26	120	126	144	36	99	117	44
2	61	82	79	99	89	193	124	113	133
3	72	}139	74	144	59	48	}173	}136	74
> 4	88		80	39	109	168			43
Total	276	247	353	378	400	445	396	366	294
P	0.30	0.96	0.33	0.24	0.75	0.66	0.56	0.64	0.63

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1984					
	14.ii	14.vi.	27.vii.	30.x.	27.xii.
1	9	54	38	19	25
2	24	102	102	49	105
3	115	46	62	}143	}78
> 4	165	75	82		
Total	313	278	285	211	203
P	0.41	0.13	0.70	0.06	0.41

TABLE 2

Estimates of instantaneous coefficient of mortality (M) for *H. laevigata* at West Island from 1971-1984 for 3 year and older age classes combined. s.e. = standard error.

Period	M	s.e.
4.xi.70 - 1.xii.71	0.14	0.10
1.xii.71 - 26.xii.72	-0.01	0.12
26.xii.72 - 17.xii.73	0.76	0.07
17.xii.73 - 10.vi.75	0.93	0.36
10.vi.75 - 21.ix.77	1.18	0
21.ix.77 - 7.ii.79	0.65 <sup>+</sup>	0
7.ii.79 - 19.xii.79	0.17	0.22
19.xii.79 - 13.ii.81	0.51	0.35
13.ii.81 - 9.xii.81	0.33	0.01
9.xii.81 - 14.xii.82	0.14	0.23
14.xii.82 - 13.xii.83	0.81	0.06
13.xii.83 - 26.xii.84	1.08	0.03

+ Poaching was reported to have occurred in October 1977. The September census recorded 118 individuals > 120 mm long and the May 1978 census only 23 (other than 20 < 125 mm long which would have grown into that size class). On the assumption that the natural mortality rate from September 1977 to May 1978 was the same as from May 1978 to February 1979, 78 individuals would have been taken by poachers. The value given is based on this assumption.

Table 3. A comparison between mean annual mortality estimates given by Shepherd et al. (1982) for marked *H. laevis* (aged c 2 years and over) and this paper for unmarked *H. laevis* aged 3 years and over at West Island. Standard errors are in brackets.

Shepherd et al. (1982)			
Period	Cormack (1964) method	Sandland & Kirkwood method	This paper
Nov. 1970 - Apr. 1974	0.26 (0.06)	0.28 (0.03)	0.31 (0.12)
Nov. 1970 - Jan. 1975	0.38 (0.17)	0.38 (0.04)	0.37 (0.15)

Table 4. Analysis of variance for regression of recruitment against SST at West I., and biomass (B) of abalone (> 120 mm long). \* = P<0.05. \*\* P<0.01.

SOURCE	DF	MS	F
<u>Excluding 1972 data</u>			
Explained	2	4448.5	6.9*
SST <sup>2</sup>	1	7641.8	11.9**
B	1	3859.1	6.0*
Residual	10	642.3	
Total	12		
<u>Including 1972 data</u>			
Explained	2	6225.5	4.3*
SST <sup>2</sup>	1	11365.5	7.8*
B	1	4347.2	3.0 n.s.
Residual	11	1450.8	
Total	13		

Table 5. Frequencies of shell damage for 1982-4. Percentages are given in brackets.

	1982	1983	1984	Total
Broken shell	19	75	145	239 (69%)
Chipped edges	10	7	11	28 (8%)
Unbroken shell	10	27	42	79 (23%)
Total	39	109	198	346

Table 6. Estimate of numbers of shells (> 3 years old) lost from the study site. Potential shell production is estimated from the mortality rates (see Methods).

	1982	1983	1984
Potential shell production (> 3 yrs)	29	145	230
95% confidence interval	0-143	129-163	216-246
Actual shell production (> 3 yrs)	27	89	168
Mean number lost from the site (%)	2 (7%)	56 (39%)	62 (27%)
No. of broken shell (> 3 yrs)	17	71	138
Estimate of numbers taken by stingrays	19	127	200
Proportion of total mortality	66%	88%	87%



Captions to text figures

- Figure 1. Map of West Island and adjoining waters. Estimated mean densities (in numbers  $100\text{ m}^{-2}$ ) of H. laevigata at the study site and on the boulder reef between West I. and the mainland. Upper left inset shows where neighbouring populations of H. laevigata on Fleurieu Peninsula occur; the dashed lines indicate their extent.
- Figure 2. Gauge used to measure and record in situ on a plastic strip the length of an abalone.
- Figure 3. Plots showing (top) change in population size of all accessible individuals, biomass of individuals  $\geq 120\text{ mm}$  long, (middle) fluctuations in numbers of each newly recruited age class in its second and third years (born on 1 January of the year indicated and (bottom) changes in the annual natural mortality rate from 1971 to 1984.
- Figure 4. (upper) Variation of mean maximum summer sea temperatures at West I., and mean maximum summer air temperatures at Victor Harbor from long term means for 1965 to 1985.  
(lower) Variation of maximum summer ocean temperatures at Cape Northumberland, S.A. from long term means for 1974-1985.
- Figure 5. Plot of recruitment strength against sea temperature anomalies at West I.
- Figure 6. Correlation coefficients between annual natural mortality rates and numbers of individuals (a)  $\geq 2$  years old, and (b)  $\geq 3$  years

old for lag time periods up to 24 months.

Figure 7 Size frequency distribution of dead shells of H. laevigata collected from 1982-4 in three categories. The inset compares the size frequency distributions of dead shell (continuous line) with the living population (dashed line).

Figure 8 Number of sightings of stingrays and octopuses during visits to West I. from 1982 to 1984.

Figure 9 Plot of number of intact shells found against sightings of octopuses and of numbers putatively taken by stingrays against sightings of stingrays for 1982-4.

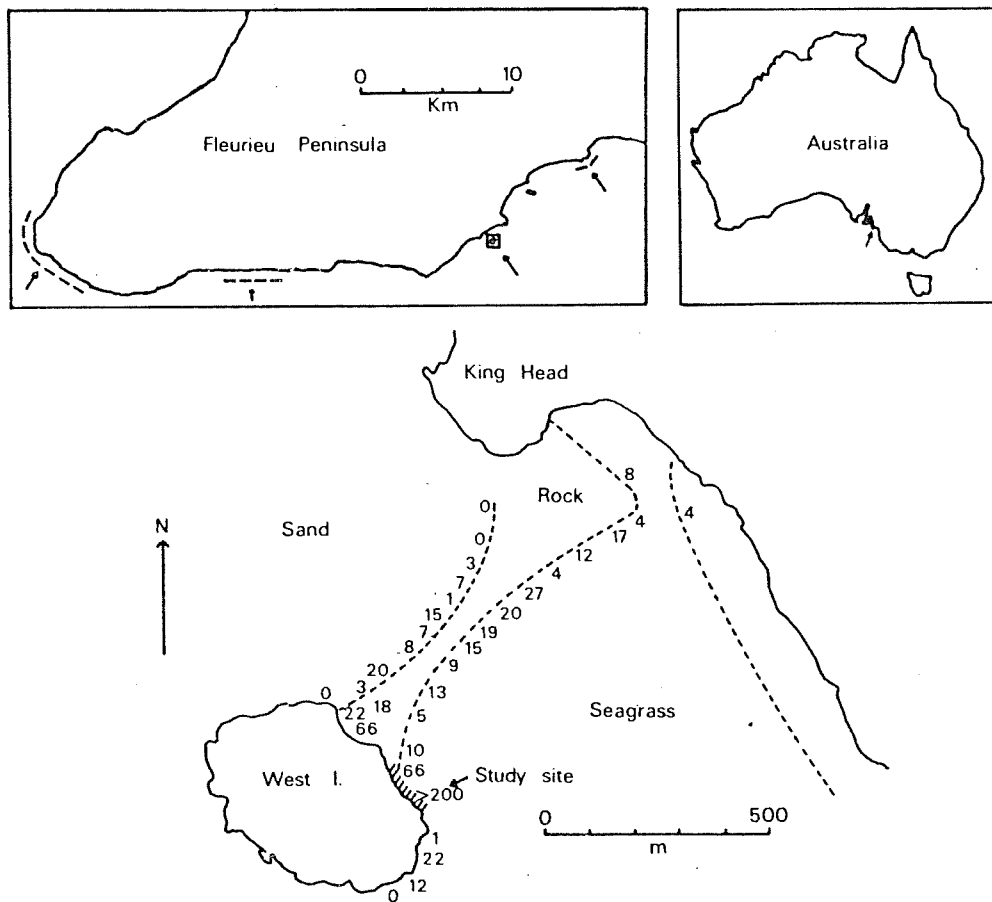


Fig. 1

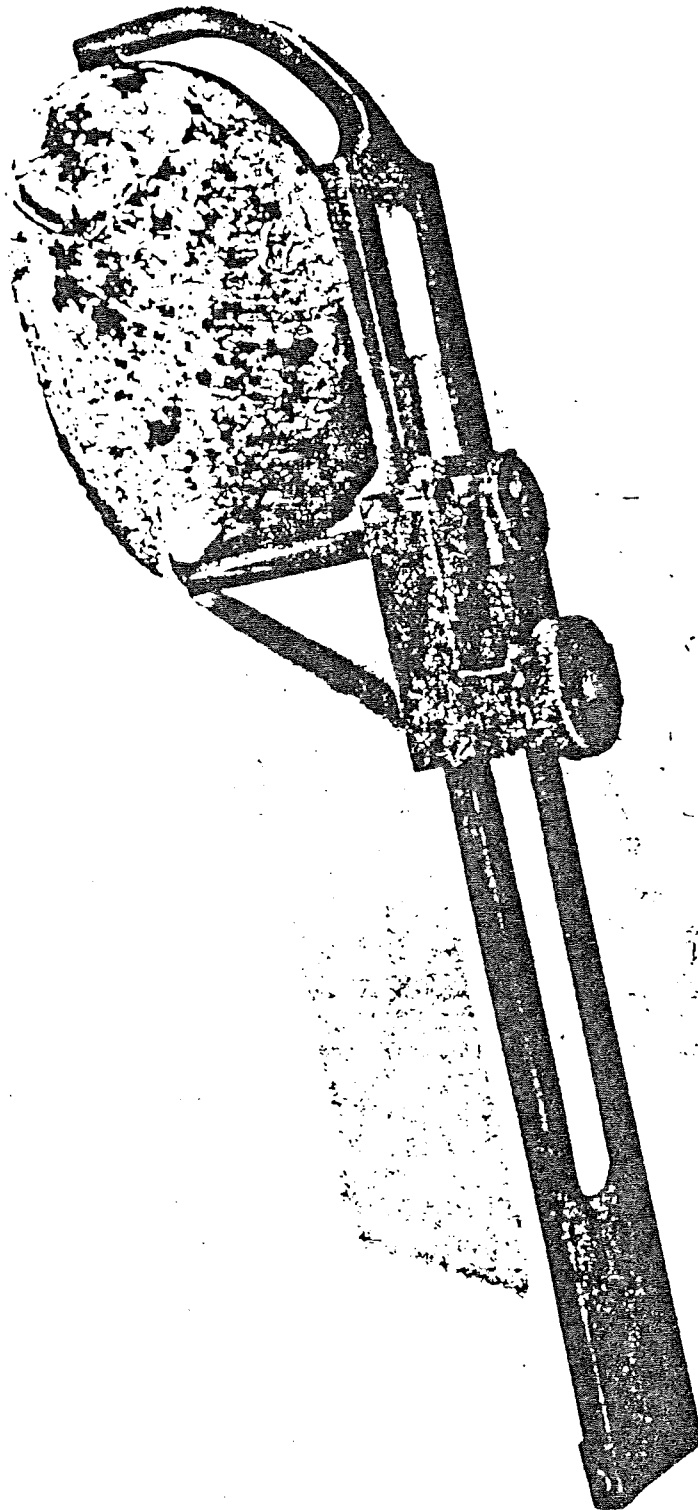


Fig. 2

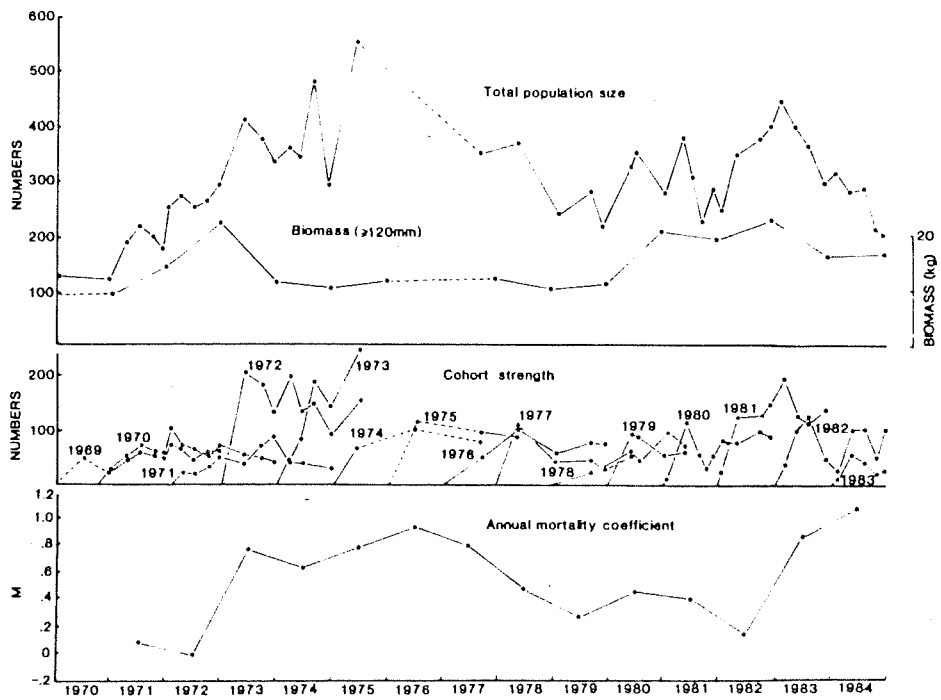


Fig. 3

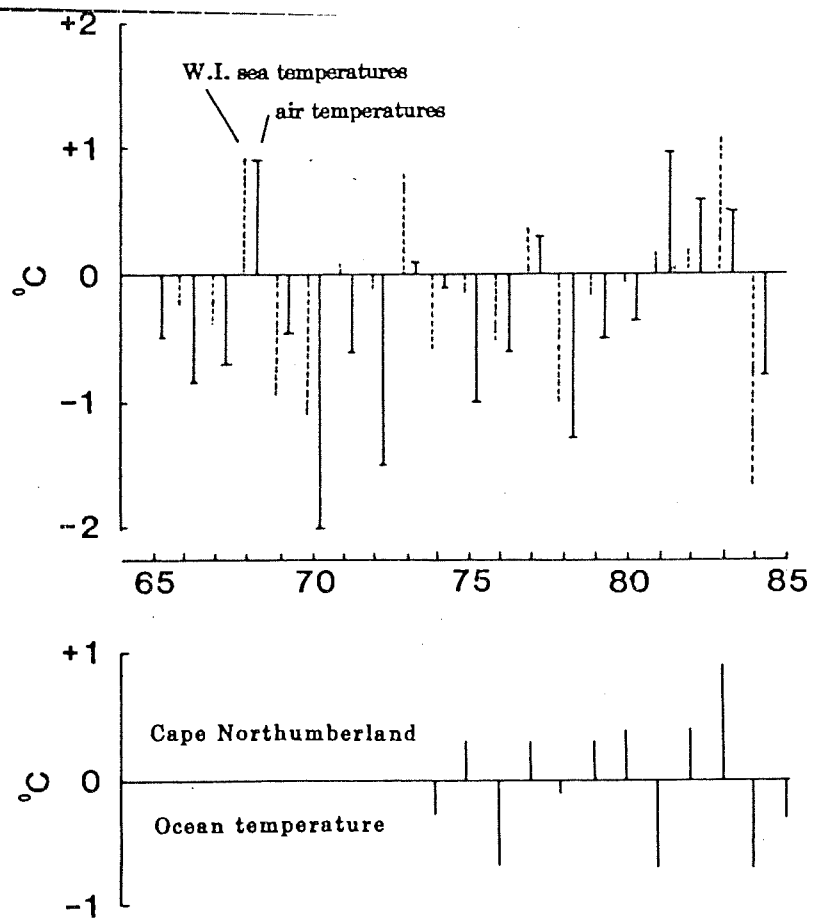


Fig. 4

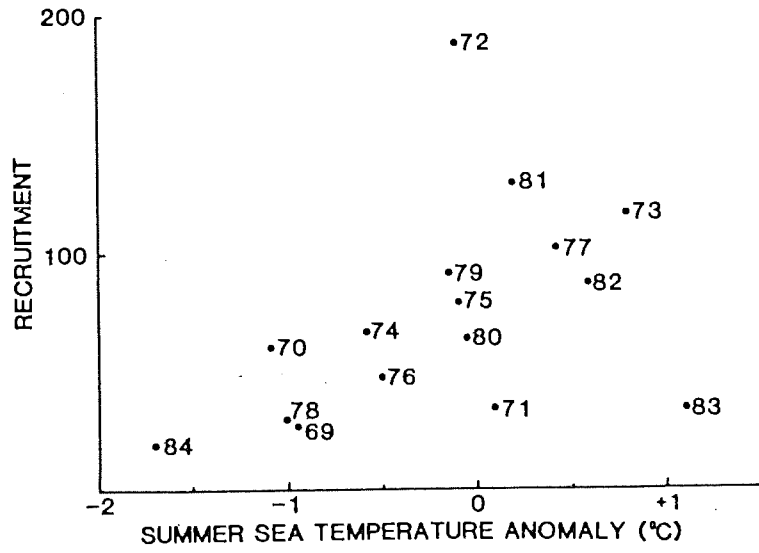


Fig. 5

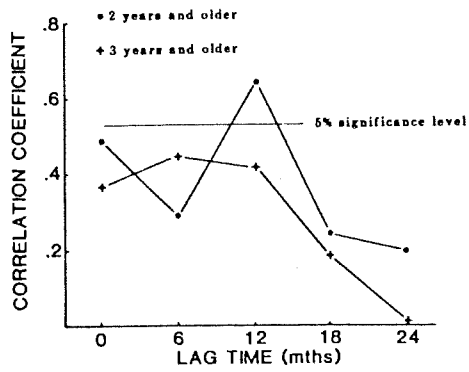


Fig. 6

Fig. 7

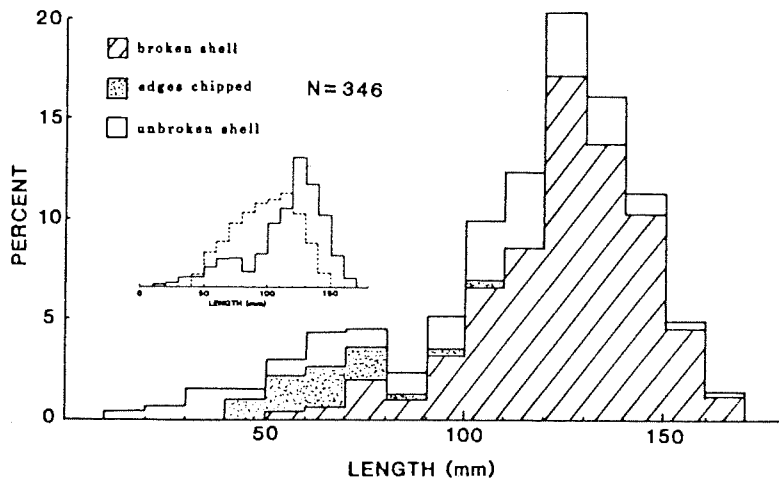
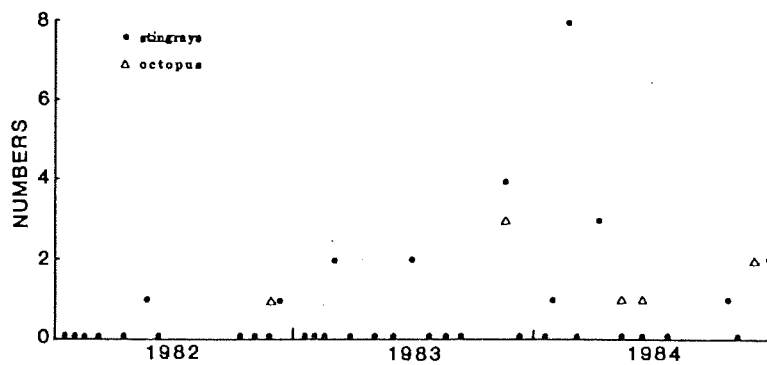


Fig. 8



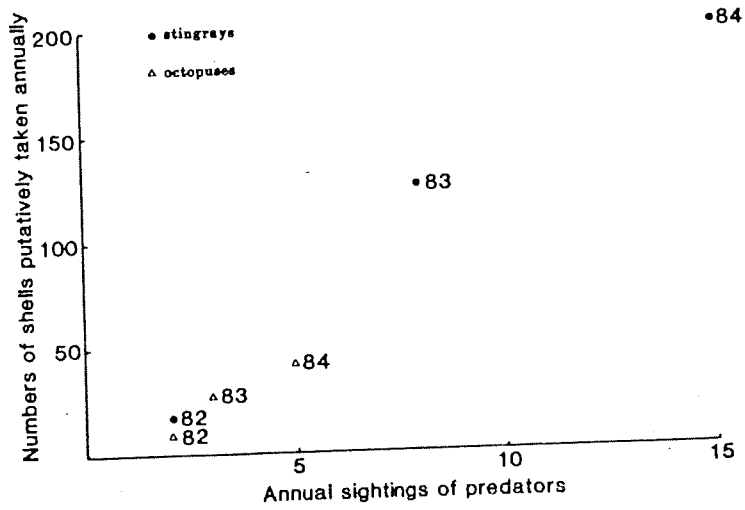


Fig. 9