J. Exp. Mar. Biol. Ecol., 1987, Vol. 106, pp. 243–263
Elsevier

JEM 00836

Experimental evidence for limited dispersal of haliotid larvae (genus *Haliotis*; Mollusca: Gastropoda)

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(Received 21 July 1986; revision received 10 November 1986; accepted 26 November 1986)

Abstract: The literature on haliotids generally assumes that these organisms have a short pelagic larval life with dispersal powers limited only by the time available before settlement. The results of an experiment designed to test this assumption are presented. The density of mature *Haliotis rubra* Leach was experimentally decreased along a 90 m section of shoreline. The resulting effect on recruitment patterns was examined in comparison with previous recruitment patterns. The results indicate that haliotid larvae may be strongly benthic with limited patterns of dispersal.

Key words: Abalone; *Haliotis*; Mollusca; Larva; Dispersal; Recruitment

INTRODUCTION

No studies on the dispersal ability of haliotid larvae have been published despite the fact that managers of haliotid (abalone) fisheries around the world are concerned with the possibility of recruitment failure (Mottett, 1978). The paucity of work in this area is due to the difficulty of finding haliotid larvae and juveniles within their natural environment (Tomita *et al.*, 1977; Breen & Adkins, 1980; Prince & Ford, 1985). From observations made under laboratory conditions it has generally been assumed that the lecithotrophic haliotid larvae are pelagic and disperse widely (Mottett, 1978; Fedorenko & Sprout, 1982; Sluczanowski, 1984; Tegner & Butler, 1985).

Recently developed techniques have made it possible to obtain samples of large numbers of haliotids within months of their settlement (Prince & Ford, 1985; Shepherd & Turner, 1985), allowing patterns of recruitment to be observed directly. Observations of recruitment patterns have indicated that they are extremely variable on a spatial scale of 20–200 m (Prince, unpubl. data). One explanation for this observation could be that larval dispersal is more restricted than has been assumed in the literature. Pelagic larvae are the most widespread form of larvae amongst benthic marine invertebrates (Thorson, 1950; Mileikovsky, 1971); free non-pelagic larvae (demersal development larvae) have,

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however, been found in a range of marine organisms (e.g. see Millar & Hollis, 1963; Pearse, 1969; Gerrodette, 1981; Olson, 1985) including gastropods (e.g. see Shuto, 1983).

The ability to disperse is a major factor affecting the potential of species to recolonize areas from which they have been removed. This ability is of particular importance for commercially caught species (Mileikovsky, 1971) as it directly effects the resilience of a species to exploitation. The objective of the present study was to test whether larval dispersal may be relatively limited in natural populations of haliotids. A number of studies have tested this premise for a range of marine organisms other than haliotids by experimentally removing or introducing reproductive stock and observing subsequent settlement or recruitment patterns (Anderson & North, 1966; Dayton, 1973; Sebens, 1983; Dayton *et al.*, 1984; Olson, 1985; Vandermeulen & DeWreede, 1986).

No techniques exist for measuring directly abalone settlement. Connell (1985), however, presented evidence to suggest that, except at very high densities, invertebrate recruitment patterns were likely to reflect settlement patterns accurately. This principle, and the possibility of directly measuring haliotid recruitment using the technique of Prince & Ford (1985), suggested the possibility of experimentally manipulating breeding stock to test the dispersal ability of haliotid larvae. The current paper describes an experiment in which the density of mature *Haliotis rubra* Leach, was reduced along a 90 m section of shoreline and the resulting effect on juvenile recruitment examined. The logistics of conducting such an experimental programme within the natural environment are great and because of this replication was impossible. An attempt has, however, been made to use previous recruitment patterns in the same area as a form of temporal replication. The assumption is that patterns in the age structure of an area are the result of breeding stock density prior to experimental manipulation. Therefore they may give an historical comparison which can provide information as to the likely pattern of settlement without experimental manipulation.

H. rubra is ideally suited for this sort of experimental design. The movement of juvenile *H. rubra* is known to be extremely restricted. At a nearby site, in a boulder habitat similar to that used in this experiment, 6 to 50-mm (maximum length) abalone were found to move < 10 m from the point of release over 12 months, while 50 to 127-mm animals generally moved < 30 m in the same time (White & Whyte, pers. comm.). If factors such as growth and mortality are assumed to act relatively uniformly, within similar habitats on a spatial scale of hundreds of metres, the density of successive size classes can be expected to preserve patterns of past recruitment. These past patterns have been used in this experiment to provide a basis for comparing the experimental with the previously undisturbed state. While this does not meet the rigorous requirements of an experimental control or replication the logistics of this process are feasible.

The hypothesis being tested by this experiment is that the abundance of abalone recruitment is related to the immediate density of adult abalone. The logic is that if abalone larval dispersal is relatively large, then abalone recruitment will not necessarily

depend on the immediate density of breeding stock. If larval movement is, however, restricted, then the occurrence of abalone recruitment will be determined by whether or not breeding abalone are present in an area.

Materials and Methods

AREA STUDIED

The area studied at Ninepin Point, Tasmania (43°17′S : 147°10′E) is a uniform section of rocky coastline extending 70 m from high water mark to a depth of 6–9 m. The bottom is composed of three layers of boulders resting on silt. The boulders are of irregular shape and mostly 30–40 cm greater diameter by 10–20 cm lesser diameter.

The macroalgal community of the area has three strata; the upper strata (> 1 m) consists of *Macrocystis pyrifera* (L.) C. Agardh, the middle strata (0.15–1.0 m) is dominated by the species *Acrocarpia paniculata* (Turn.) Aresch., *Cystophora moniliformis* (Esper), Wom. & Niz., and *Sargassum verruculosum* (Mertens) C. Agardh, the lowest strata (0–0.15 m) is dominated by encrusting corallines. On the exposed surface of the boulders these corallines are overgrown by filamentous algae including *Cladophora* sp., *Ceramium* sp., *Polysiphonia* sp. and *Calithamnion* sp., and small fleshy algae of the genera *Zonaria*. In depths > 6 m algae of the genera *Peyssonnelia*, *Thamnoclonium* and *Caulerpa* commonly overgrow the crustose corallines which are abundant at these depths.

In this area *Macrocystis pyrifera* is of limited importance, being confined to a narrow (5–10 m in width), diffuse and irregular band ≈20 m from the shoreline in depths of 2–3 m. As a consequence, despite the presence of *M. pyrifera*, in depths < 4 m the algal community is typical of a fucoid association indicative of slight to moderate wave action (Sanderson & Thomas, 1987). This is in contrast to depths > 4 m where the characteristics of the algal community change, and only the lowest strata is found.

This entire section of shoreline has carried a natural population of *Haliotis rubra* at sufficient densities to support continuing amateur and professional fishing over the past 15 yr, suggesting regular recruitment of abalone.

BREEDING STOCK REMOVAL

The existence of recent recruitment and the size of the smallest abalone present before the experiment were established with one day sampling (3 August 1985) using the anaesthetic technique (detailed below). Following this the central 90 m section of shoreline was marked out for the removal of abalone breeding stock. To aid in the allocation of diving effort during the removal process, this area was divided into three segments, Sites 4, 5 and 6, respectively (Fig. 1), each ≈30 m long. These were delineated with chain laid on the seabed perpendicular to the shore from low water mark to the edge of the sandy substratum.

On five occasions between 10 August 1985 and 18 September 1985 all abalone found

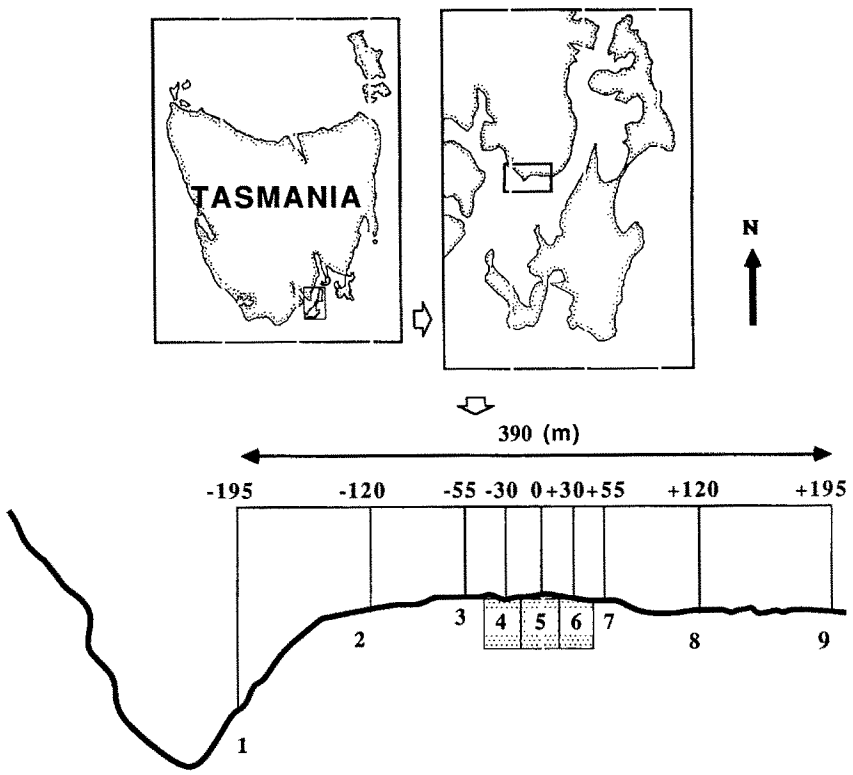

Fig. 1. The location and layout of the study site at Ninepin Point, Tasmania: shaded area indicates the area from which abalone were removed and the numbers indicate sampling sites; distances (m) are given from the centre of the removal area.

of >60 mm maximum shell length were removed from each of the three sections by divers. Disturbance of the substratum during collection was minimal as abalone were only taken from the exposed boulder surfaces and no boulders were moved during the searches. It was recognized that a proportion of the >60-mm abalone would not be detected by these searches, but minimal disturbance of the substratum was considered more important than maximal reduction of the population. The maximum length of each abalone captured was measured to the nearest millimetre. The number removed from each of the three 30-m segments and the total diver-hours expended in each area was recorded for each of the first four searches. The fifth and final search was of a shorter duration (total diver-h = 4.5) and on this occassion the catch and effort was not separated by area.

BREEDING STUDIES

From the initial removal (10 August 1985) subsamples of 20 abalone from each 10-mm size class were retained for gonad index studies. The methods used for this study

are based on those of Hayashi (1980). After fixation in 10% formalin the visceral mass was sectioned beneath the visceral coil and the cross section placed against clear plastic and drawn. The relative areas of gonad and hepatic gland in the cross section were calculated by weighing the plastic outlines. The gonad index was calculated as the percentage of the area of the cross section made up by the gonad.

A further sample of 83 abalone, covering the size range indicated by the gonad index study to be mature, were collected between 10–16 September 1985 for analysis of fecundity. The fecundity at the site studied was also measured after the removal of breeding stock to determine the time of spawning at the site.

The method used to estimate fecundity was based on that of Sainsbury (1982). After fixation in 10% formalin the gonad was dissected from the hepatic gland and gently teased apart into 50–250 ml of sea water. The water was agitated until all the eggs were free and evenly dispersed; two or three 0.5 to 1.0-ml samples were then taken. Each sample was placed in a counting chamber marked with a grid and the yolked eggs in five standard squares were counted. Total fecundity was calculated by multiplying out the various subsampling factors.

POST REMOVAL SAMPLING

In February–March 1986 the abalone populations at nine sites were sampled. The sites (Fig. 1) covered 390 m of shoreline, and were situated at the centre of the segment of shoreline from which the breeding stock was removed (0 m, Site 5) and 30 m (Sites 4, and 6), 55 m (Sites 3 and 7), 120 m (Sites 2 and 8), and 195 m (Sites 1 and 9) either side of the centre. This spacing was selected so as to maximize the probability of observing any effect caused by removing the breeding stock.

The anaesthetic technique detailed by Prince & Ford (1985) was used to sample the abalone at these sites. Twenty areas of 1 m^2 at each site were selected by throwing a quadrat from an anchored vessel. Stratification was achieved between sites by anchoring the vessel 10 m offshore while selecting the initial 10 squares at each site, and 35 m offshore while selecting the remaining squares. If the square landed on an area where no substratum could be gathered, the boulders being too large or the substratum being entirely sand and silt, the square was retrieved and re-thrown. From each selected area a diver collected all the substratum possibly suitable for abalone, principally boulders and kelp. The few boulders too large to lift to the surface were searched underwater and all abalone collected.

The substratum material was placed in bins and bathed in a 1% solution of ethanol in sea water for a minimum of 10 min. This material was then brushed with a soft brush before being removed from the solution. After all the solid substratum removed from a square had been soaked, the contents of the bins were drained through 15-mm and 0.5-mm sieves. Abalone retained by the coarser sieve were collected and the sample held by the smaller sieve was returned to the laboratory for examination. These samples were washed through sieves of 9-, 4-, 2- and 1-mm aperture and the abalone preserved. The maximum shell length of all abalone collected were measured to the nearest 1 mm.

The length frequency data from the samples were analysed using the Macdonald and Pitcher mixture analysis 'Mix' (Macdonald & Pitcher, 1979; Macdonald & Green, 1985). The cut-off points between the different size distributions of abalone described by this analysis were taken as the points where two consecutive distributions overlapped. These points were calculated using the formula:

$$X = [(\bar{x}_2 + \bar{x}_1) \times 0.5] + [(s_1^2 \times s_2^2) \times \log_e (\pi_1/\pi_2)/(\bar{x}_2 - \bar{x}_1)]$$

where X is the cut-off point (mm) and $\bar{x}_i$, s_i^2, and π_i are the estimated means, standard errors, and proportions of the i-th distribution, respectively.

The densities of abalone detected showed a tendency to be positively skewed about the mean. A $\log(Y + 1)$ transformation was used to normalize the data. The differences in densities between areas was tested with a two-tailed Student's t-test using a significance level of 0.05. This method was also used to test the significance of correlations between adult and juvenile densities.

Results

BREEDING STUDY

Analysis of the gonad index of abalone collected from the research site on 10 August 1985 showed that for the size classes examined (>60 mm) the index increases with size up to the length of 100 mm; a sharp increase was observed between 90 and 100 mm. Maximal values were found in abalone of 100–145 mm maximum length. The relationship between fecundity and maximum shell length for animals collected 10–16 September 1985 was best described by a single variable regression:

$$F = (0.028 \times ML) - 2.415$$

where F is fecundity measured in millions of eggs and ML is maximium shell length in millimetres. This relationship was found to be highly significant ($r = 0.62$; $n = 83$; $P < 0.001$). The intersection of this curve with the x-axis is at 87 mm, which is in relatively close agreement with the results obtained by examining the gonad index. These results indicate that the onset of sexual maturity in this area probably occurs when the abalone attain the length of 87 mm and that by the length of 100 mm virtually all the abalone are sexually mature.

A sample of 45 mature female abalone collected on 27 September 1985, indicated that a widespread spawning had occurred in the study area prior to this date. Over 50% of the gonads showed signs of extensive spawning, 26% had fecundities <5% that predicted by the above relationship. For this sample the relationship between maximum length and fecundity was not found to be significant ($r = 0.23$; $n = 45$; $P > 0.1$). This timing is consistent with the observations of Harrison & Grant (1971) made for

Tasmanian populations of *H. rubra* and suggests that a general spawning occurred within 9 days of the final search for breeding stock. The water temperature at the site studied at this time was $\approx 13\,^{\circ}C$.

BREEDING STOCK REMOVAL

Between 10 August 1985 and 18 September 1985 divers spent 85.8 diver-h searching for abalone. A total of 3584 abalone were removed from the 90-m section of shoreline encompassing Sites 4–6, of which 3274 (91%) were > 87 mm (Fig. 2). Over the entire area catch rates fell from 104.0 > 87 mm abalone $\cdot h^{-1}$ during the initial search to 9.8 > 87-mm abalone $\cdot h^{-1}$ during the final search (Fig. 3). Using the number of abalone caught in each area and the size of the areas (1793, 1987 and 1674 m^2 for Areas 4, 5 and 6, respectively), the searches can be calculated to have reduced the density of mature abalone by 0.54, 0.51 and 0.77 abalone $\cdot m^{-2}$ in each area respectively. Catch rates declined from 98.7, 92.6, and 127.1 > 87-mm abalone $\cdot h^{-1}$ during initial searches, to 10.2, 7.4 and 16.2 > 87-mm abalone $\cdot h^{-1}$ in Areas 4, 5 and 6, respectively, during the fourth search.

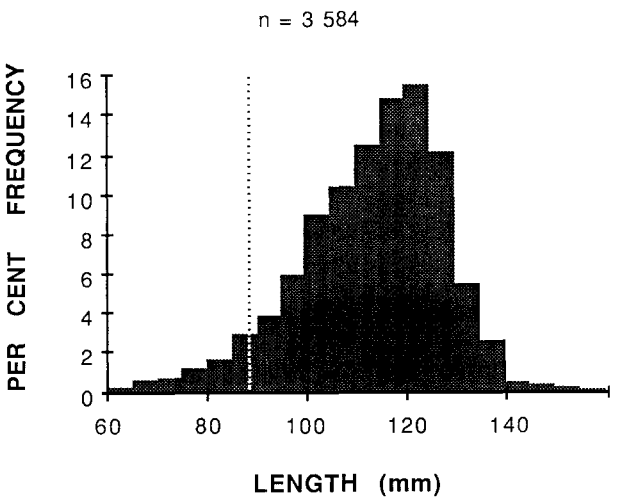

Fig. 2. Length–frequency histograms for *Haliotis rubra* collected during searches of the removal area: dotted line indicates the size of first maturity (87 mm).

Accepting the catch rates as an index of relative abundance the estimated decrease in abundance of mature abalone in each area between the first and fourth visit is 89.7, 92.0 and 87.3%, respectively. From these data it can be estimated that the density of mature abalone within each area before the searches was ≈ 0.60, 0.55, and 0.88 abalone $\cdot m^{-2}$, respectively. It can also be estimated that after the searches the remaining density of mature abalone in each area was 0.06, 0.04, and 0.11 abalone $\cdot m^{-2}$,

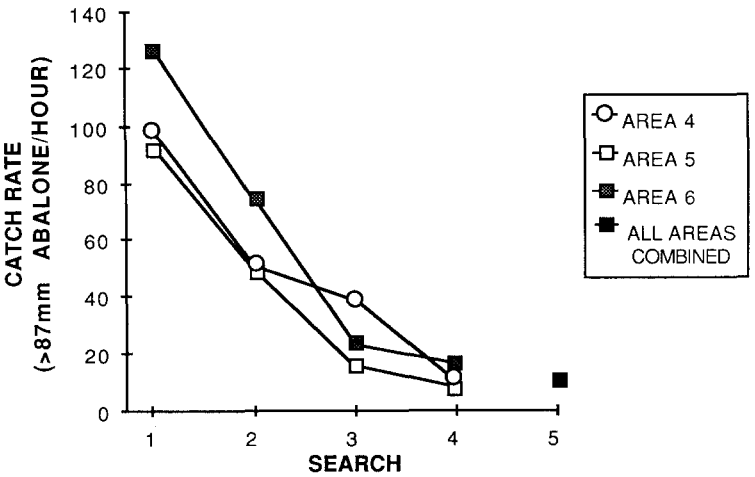

Fig. 3. Catch rates of *Haliotis rubra*, in each section of the removal area, during each period of searching: data were not separated by area for the fifth search.

respectively. In making these estimations only the catch rate data from the first four searches have been used, as these data were not separated by individual area during the short (4.5 diver-h) final search. The final catch (44 > 87-mm abalone) has been proportioned equally between the areas. Any bias caused by this process is likely to be negligible due to the small number of abalone removed by the final search.

The movement of *H. rubra* is known to be relatively limited and widespread spawning commenced within 9 days of the final search. So it can be safely assumed that the estimated densities of mature abalone after the searches approximate the density that was present in each area during spawning.

POST REMOVAL SAMPLING

Fig. 4A shows the density of mature (>87 mm) abalone measured at each site in February–March 1986, four months after spawning had occurred. Sites 1–3 had a generally low level of mature abalone when compared with Sites 7–9. The effect of removing breeding stock from Sites 4–6 (Sites 4–6 pooled) was still clearly evident at the time of sampling, with the density of mature abalone being significantly lower ($t = 4.15$; $P < 0.001$) than the mean density at the other sites (Sites 1–3, 7–9 pooled). The effect of migration back into the area since the removal is indicated by the shape of the depression in densities, with the highest value (Site 6) being adjacent to the highest adjoining outside value (Site 7) and the lowest value being at Site 5, furthest from the source of immigrating abalone.

Fig. 5 shows the length frequency histograms for all 0 to 60-mm abalone collected during anaesthetic sampling in 1-mm size classes. The figure presents the results of preliminary sampling conducted in August 1985 and the sampling conducted in

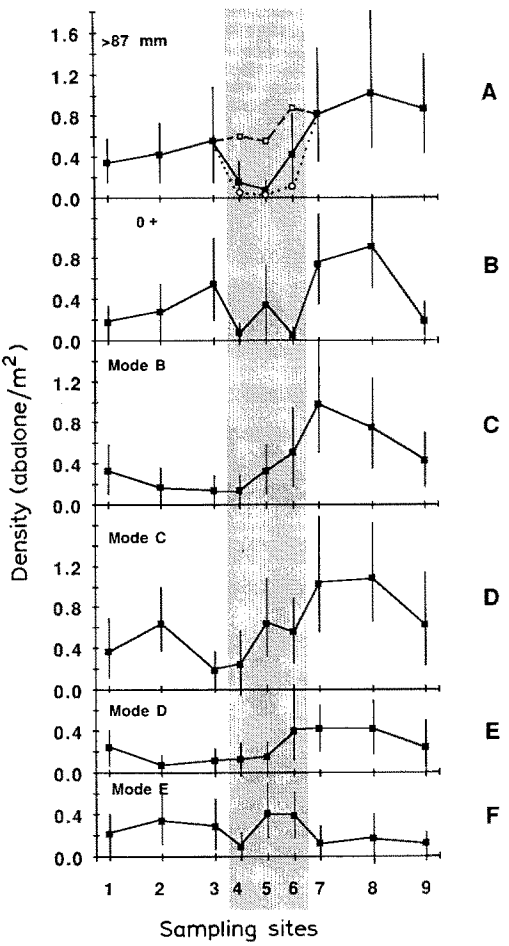

Fig. 4. The density of *Haliotis rubra* measured at each sampling site in February–March 1986, using the anaesthetic technique (solid line): A, >87-mm abalone, broken line indicates estimated density before searches, dotted line indicates estimated density during spawning; B, 0^+ mode; C, Mode B; D, Mode C; E, Mode D; F, Mode E; bars indicate ± 95% confidence interval; shading indicates sites from which mature abalone were removed.

February and March 1986. These latter data are shown grouped for Sites 1–3, 4–6, 7–9 and for all sites pooled.

When the Macdonald & Green (1985) MIX program was used to describe the 0 to 42-mm length-frequency data the best fit was achieved with 10 log-normal size distributions, with means at 3.3, 8.4, 12.3, 15.1, 19.7, 23.7, 27.7, 33.2, 36.4, and 40.0 mm ($\chi^2 = 7.54$; d.f. = 13; $P = 0.87$). Because the smallest abalone collected during the preliminary samples, in August 1985, was 5 mm in length the smallest size group observed in February and March ($\bar{x} = 3.3$ mm) clearly settled after the removal of

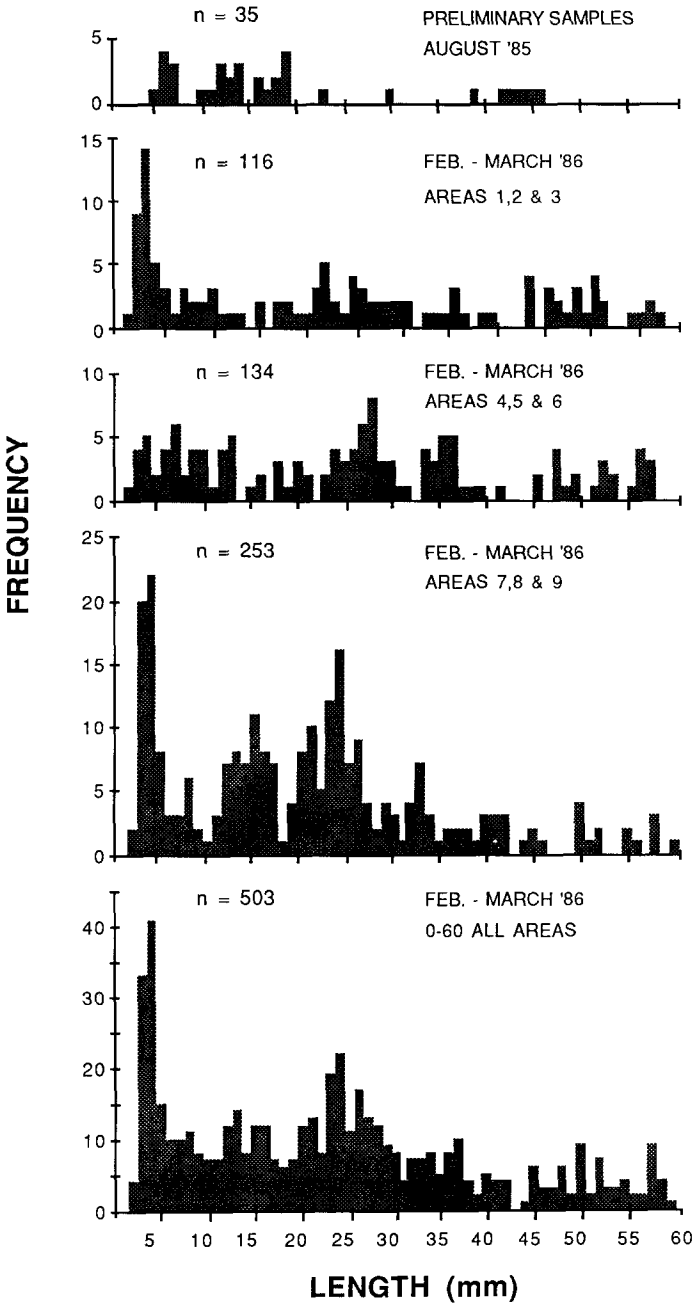

Fig. 5. Length–frequency histogram for all 0–60 mm *Haliotis rubra* sampled with the anaesthetic technique during August 1985 and February–March 1986; the February–March samples are grouped for Sites 1–3, 4–6, 7–9, and all sites combined.

breeding stock. The estimated cut-off point between the first and second distribution is 6 mm.

The next best description of the 7 to 42-mm data grouped the 2nd–4th, 5th–7th and 8th–10th of the former distributions, respectively, and described these data as three distributions. In this latter analysis the estimates converged with the estimated means of each distribution being 14.4, 25.0, and 36.1 mm ($\chi^2 = 37.1$; d.f. = 30; $P = 0.174$). To increase the numerical abundance of each size class this grouping of the smaller distributions has been used. The cut-off points between the three larger distributions (17 and 31 mm) have, however, been calculated using the estimated parameters of the smaller component distributions. The size group 43–60 mm is clearly distinct from the smaller size groups and has been treated as a separate size class.

This cursory analysis of the length–frequency histogram is not meant to imply an age for any size group besides the 0 to 6-mm class. This smallest class was clearly not present in the August 1985 samples, but settled after the searches, consequently it can be concluded that they represent at least some portion of the 0^+ age class. No age can be attached to the other size classes. If growth rates are, however, assumed to be relatively uniform within the area studied it can safely be assumed that each size class represents some unknown grouping of ages. If this is accepted, and mortality is also assumed to be relatively uniform over the research area, each size group can be used to indicate the recruitment pattern which occurred over some period of the past. For this analysis the 0 to 6-mm size group will be referred to as the 0^+ and the size groups 7 to 17, 18 to 31, 32 to 42 and 43 to 60-mm will be referred to as Modes B, C, D and E, respectively.

Fig. 4B shows the measured density of the 0^+ mode across the sampled sites. The mean density for Sites 4–6 (Sites 4–6 pooled) was significantly lower than the mean of the other sites (Sites 1–3, 7–9 pooled; $t = 3.52$; $P < 0.001$). The density for the 0^+ size group at Sites 1–3 was also generally lower than at Sites 7–9. These results show that a reduced level of recruitment occurred at Sites 4–6 following the removal of mature abalone. This effect appears to have been extremely localized, with the reduction in recruitment only being evident within the removal area. This pattern corresponds to the density pattern of adult abalone at the time of spawning.

In contrast to the observed 0^+ densities, the density patterns observed for each of the other modes were generally similar to the pattern of mature abalone, estimated to have existed prior to the removal process. With the exception of Mode E all had higher values at Sites 7–9 and their density declined relatively smoothly towards Sites 1–3 (Fig. 4C–F). The density of Mode E showed no obvious trends across the sites. For each of these size classes no significant difference was found between the mean densities at Sites 4–6 (Sites 4–6 pooled) and the mean density of the sites outside (Sites 1–3, 7–9 pooled) the removal area (Mode B; $t = 1.18$; $P > 0.1$, mode C; $t = 1.22$; $P > 0.1$, Mode D; $t = 0.287$; $P > 0.1$, Mode E; $t = 1.13$; $P > 0.1$). These data indicate that no historical precedence exists for the recruitment pattern observed following the removal of breeding stock.

TABLE I

Estimated correlations between the density of the 0^+ size group, modes B, C, D and E, and the estimated density of mature (>87 mm) abalone before and after the searches.

	Regression variable X–density of >87 mm abalone			
Regression variable Y	Regression equation	Correlation coefficient (r)	t-statistic ($n = 9$)	2-tailed significance
Before removal				
0^+	$y = -0.01 + 0.55x$	0.42	1.22	0.256
Mode B	$y = -0.17 + 0.87x$	0.70	2.59	0.032
Mode C	$y = 0.03 + 0.84x$	0.63	2.15	0.064
Mode D	$y = -0.07 + 0.47x$	0.78	3.29	0.011
Mode E	$y = 0.34 - 0.16x$	0.30	0.83	0.430
After removal				
0^+	$y = 0.08 + 0.60x$	0.73	2.83	0.022
Mode B	$y = 0.20 + 0.46x$	0.58	1.88	0.096
Mode C	$y = 0.36 + 0.51x$	0.61	2.04	0.076
Mode D	$y = 0.16 + 0.17x$	0.45	1.33	0.219
Mode E	$y = 0.32 - 0.18x$	0.54	1.70	0.128

Linear regressions of the density of these smaller size classes at each site against the density of mature abalone at each site, both before the searches and at the time of spawning, have been estimated (Table I). In this analysis the estimates of the initial density of mature abalone at Sites 4-6 before the searches (0.60, 0.55, and 0.88 abalone $\cdot$ m^{-2}, respectively) have been used along with the estimated densities during spawning (0.06, 0.04 and 0.11 abalone $\cdot$ m^{-2}, respectively). The density of mature abalone estimated by the post removal sampling at Sites 1–3 and 7–9 have been used as the density at these sites both before the searches and at the time of spawning.

With the exception of Mode E, all the modes showed a positive correlation with the density of mature abalone both before and after the removal process. The density of Mode E was not significantly correlated with the density of mature abalone before the searches ($r = 0.30$; $n = 9$; $P > 0.1$) nor at the time of spawning ($r = 0.54$; $n = 9$; $P > 0.1$). The relationships between the density of mature abalone before the searches and the densities of Modes B ($r = 0.70$; $n = 9$; $P < 0.05$) and D ($r = 0.78$; $n = 9$; $P < 0.05$) at each site are significant, while the correlation with Mode C is high but not significant at this level ($r = 0.63$; $n = 9$; $P = 0.064$). The density of 0^+ at each site was not significantly correlated with the density of mature abalone before the searches ($r = 0.42$; $n = 9$; $P > 0.1$).

In direct contrast to the above, the density of mature abalone at each site during spawning was significantly correlated only with the density of the 0^+ ($r = 0.73$; $n = 9$; $P < 0.05$). These results indicate that the density pattern observed for the 0^+ was most closely related to the densities of mature abalone that existed at the time of spawning, while the density patterns of Modes B, C and D were most closely related to densities of mature abalone that existed before the removal process.

Discussion

The results of this experiment clearly demonstrate that for *H. rubra* the density of recruitment is related to the immediate density of spawning abalone. The density of recruitment (the 0^+ mode) was significantly lower inside the area from which spawning stock were removed, than outside the area, a pattern which was not evident in the size groups of abalone spawned before this experiment was conducted. In addition, the density of recruitment both inside and outside the area was significantly correlated with the density of breeding stock at each site. Abalone populations have been observed to be stable over time (Hines & Pearse, 1982). Thus, the density pattern of the spawning stock before the searches was probably similar to those that existed when modes B, C, D and E were recruited. The density pattern of three of these size classes were more strongly correlated with this previous pattern of breeding stock than with the pattern created by the searches. This is consistent with the finding that for *H. rubra* recruitment is directly related to the immediate density of spawning abalone. The fact that the density of the fourth and oldest size class was not correlated with either density pattern of spawning stock may indicate that some change has occurred in this abalone population over time, or the effect of movement over time.

Patterns of recruitment may arise from two causes, differential settlement or differential mortality after settlement (Keough & Downes, 1982). Connell (1985) postulated that at high settlement densities, density dependent mortality may affect recruitment. In the present study density dependent mortality would have had a smoothing effect, producing a pattern of recruitment more uniform than the settlement pattern. This would have reduced the likelihood of observing a relationship between spawning stock and recruitment but it can be rejected as being the cause of this relationship.

It is possible to hypothesize that some other form of differential mortality acting on the recruited juveniles is the causal agent of the observed pattern. To do this it is, however, necessary to take into account the significant relationship between spawning stock density and recruitment density. Any hypothesized form of differential mortality must be inversely related to the density of adult abalone. In the literature there is no indication of any biological factor associated with adult abalone which promotes the survival of juvenile abalone after settlement. Consequently, it would appear unlikely that differential mortality can explain the observed recruitment pattern and that such patterns reflected the abundance of settlement at each site.

Accepting that the recruitment densities observed reflect actual settlement patterns four explanatory models can be postulated to explain these patterns: (1) settlement of abalone larvae is random; (2) settlement is attracted by physical, chemical or biochemical cues independent of the adult stock; (3) settlement is attracted by physical, chemical or biochemical cues associated with the adult abalone; (4) dispersal of larvae is extremely restricted (Underwood, 1979).

The first and second model are easily dismissed as being incompatible with the significant correlation that was observed between recruitment density and the density

of adults. The third model cannot be entirely discounted. Abalone larvae are known to settle on surfaces of coralline algae (Shepherd & Turner, 1985). It is possible that grazers such as abalone play an important rôle in keeping these surfaces free from epiphytes and available for settling larvae. Larvae have also been shown to settle on the slime trails of conspecifics (Seki & Kan-no, 1981a). Both these factors could possibly attract larvae to settle around adult abalone and such a phenomenon has been observed in the laboratory for a number of other gastropods (see Underwood, 1979). It should also be noted that Underwood stresses that this does not necessarily happen in the natural environment.

In the present study adult abalone were only removed from the exposed surface of boulders during the searches and small abalone were not collected. The crustose coralline algae on the exposed surface of the boulders were overgrown with epiphytes before the searches were conducted which is in contrast to the crustose coralline algae on the under surfaces of the boulders in the area. These latter corallines showed evidence of grazing before and after the searches and it was on these surfaces that the small 0^+ abalone (< 5 mm) were usually found, suggesting that these were the settling sites. As large amounts of macroalgae other than crustose corallines were available above the boulders and these are the preferred food of *H. rubra* in this area (Prince, unpubl. data) it is improbable that the adult abalone found during the searches were grazing the coralline surfaces below the rocks or leaving many slime trails in this micro-habitat. The high proportion of the adult abalone population in the removal area, collected by searching the exposed surface of the boulders ($> 85\%$) also suggests that adult abalone spend little time in the under-boulder habitat. In contrast, small abalone (< 60 mm) were rarely observed on the exposed surfaces of the boulders (despite > 20 h night diving) suggesting that if conspecific abalone have a rôle in conditioning settlement sites it is probably the juveniles which are the more important. It should also be remembered that spawning began within 9 days of the last search, so that the time available for any increased epiphytic growth on settling surfaces was relatively restricted. For these reasons it is unlikely that the removal of adult abalone significantly affected the epiphytic growth or the number of slime trails on potential settlement sites. Consequently it is improbable that the observed recruitment patterns resulted from settlement being attracted by cues associated with adult abalone. This conclusion is supported by Shepherd & Turner (1985) who, on the basis of their field study, discounted the likelihood of abalone larvae being attracted to or by conspecific adults.

The final model which can explain the settlement pattern inferred by this study is that abalone larval dispersal at the site studied was extremely restricted. This explanation suggests that significant numbers of larvae did not travel into the removal area from the spawning stock known to have been outside the area, a distance at Sites 4 and 6 of only 15 m. The literature for haliotids assumes that abalone larvae are pelagic (Mottett, 1978; Fedorenko & Sprout, 1982; Tegner & Butler, 1985), swimming to the surface after hatching. Matthews & Volframs (1978) studied a similar body of water near the area studied and showed that in depths < 10 m water movement is primarily wind driven.

From the relationship derived by that study, between wind strength, depth and water movement, and from meteorological data (Aust. Dept. Sci., unpubl. data) it is possible to estimate the magnitude of water movements in the area during the time when the abalone were spawning as $\approx 0.005-0.038\ m \cdot s^{-1}$. The movement can effectively be considered unidirectional for periods of 48–96 h (Matthews & Volframs, 1978). This would have resulted in a gross movement of between 430 and 3300 m for every 24-h period abalone larvae spent in the water column, depending on the depth at which they occurred. The gross distance moved by a cell of water indicates a magnitude of mixing and dispersal, for pelagic larvae, that is incompatible with the localized reduction in settlement observed in this experiment. Clearly, the assumption of a pelagic larval life for *H. rubra* is not supported by the settlement pattern inferred by this study. Considering the magnitude of the water movement the inverse of this assumption is suggested by these results. That is, haliotid larvae avoid dispersal.

The assumption that abalone larvae are pelagic in the natural environment rather than demersal is based solely on laboratory observations of haliotid larvae. Under laboratory conditions the trocophore is positively phototactic and swims slowly towards the surface (Ino, 1952; Leighton, 1974; Yano & Ogawa, 1977; Tanaka, 1978). Late stage veligers exhibit "tumbling behaviour", in which large numbers assemble in vertical columns and at irregular intervals spontaneously tumble to the bottom of the tank and disperse (Leighton, 1972; Grant, 1981; Grant & Sumner, in prep.). Mariculturists take advantage of these behaviour patterns by using surface collection techniques when transferring larvae between tanks (Ebert & Houk, 1984). Under laboratory conditions settlement of larvae generally occurs between 3–11 days post fertilization depending on temperature (Ino, 1952; Leighton, 1974; Ebert & Houk, 1984). These observations have all been made during mariculture research programmes and no controlled experiments have been published which test their accuracy or relevance to natural conditions. Instead, the relevance of these observations to the natural environment has been assumed, and they have been taken to indicate that naturally occurring abalone larvae are pelagic, having a dispersal phase before becoming competent to settle (precompetent phase) equivalent to the time taken to settle in the laboratory (Mottett, 1978; Fedorenko & Sprout, 1982; Sluczanowski, 1984; Tegner & Butler, 1985).

There is, however, no certainty that such an assumption can be made (Underwood, 1979). The preferred settlement conditions for abalone are still poorly understood and can only be crudely approximated in the laboratory (T. Dix, pers. comm.; J. Grant, pers. comm.). It is known that when faced with less than optimal settlement conditions invertebrate larvae postpone settlement (Thorson, 1950). It has also been shown that the discrimination of the larvae choosing settlement substrata decreases as larval life is prolonged (Knight-Jones, 1953). Because of this, the time from fertilization to settlement observed in the laboratory may be a gross over-estimate of the average length of larval life in the natural environment, where optimal settlement conditions occur. These estimates of the length of abalone larval life should be regarded as estimates of the maximum length of larval life rather than the minimum.

The minimum possible larval life length is actually the time required by the larvae to become physiologically capable of settling (Strathmann *et al.*, 1981) and this is the correct definition of the precompetent phase (Jackson & Strathmann, 1981). For abalone this is when the third tubule forms on the cephalic tentacles, and the ctenidium and first epipodial tentacle appear within the larval shell (Grant, 1981; Seki & Kan-no, 1981b). For *H. rubra* the length of the precompetent phase is $\approx$ 106 h at 16 °C (Grant & Sumner, in prep.) although settlement in the laboratory does not normally occur until $\approx$ 142 h post fertilization. Even this does not give a true indication of what may be the minimum possible time available for dispersal. To estimate this it is necessary to consider the proportion of the precompetent phase during which the larvae are physiologically forced to swim freely. Abalone eggs are considerably heavier than water (Ino, 1952; Grant, 1981) and if dispersal occurs it is unlikely to occur before the trocophore hatch. In addition, abalone larvae are able to stop swimming and explore settlement surfaces by creeping from the time the two snout protruberances are formed (Seki & Kan-no, 1981b). For *H. rubra* the time between hatching and being capable of movement by creeping rather than swimming is only $\approx$ 43 h at 16 °C (Grant & Sumner, in prep.; J. Grant, pers. comm.).

The second difficulty in assuming that the laboratory behaviour of larvae is the same as natural behaviour, is that the simple, smooth, sterile laboratory tanks in which the larvae are held are totally divorced from the biologically and physically complex bottom on which abalone naturally occur. Also the densities at which the larvae are held are probably several orders of magnitude higher than those found naturally (T. Dix, pers. comm.; J. Grant, pers. comm.; L. Tong, pers. comm.). In these conditions it cannot be assumed that larval behaviour is normal. Even if this assumption were made, the importance of stereotyped behaviour might be lessened by numerous conditions in the field (Moore, 1975; Young & Chia, 1982). It is probable that if the behaviour of cultured larvae correspond to the behaviour of larvae in the natural environment, then it may correspond to the behaviour of larvae that have hatched in smooth, simple conditions. It has been demonstrated that invertebrate larvae can be capable of a number of behaviour patterns stimulated by different settlement prospects (e.g., Harrigan, 1972; Young & Chia, 1982). A possible hypothesis is that larvae in the laboratory are attempting to disperse widely because they do not receive the cues which indicate the proximity of natural settling sites, while larvae that detect these cues may avoid or minimize dispersal.

Restricted dispersal of larvae is favoured amongst benthic marine invertebrates when the resources they require are uniformly available (Menge, 1975) and relatively free of temporal variation (Palmer & Strathmann, 1981). In this situation larvae that disperse have a lower probability of finding suitable habitats than non-dispersing larvae and face greater risks while they search (Sebens, 1983). After settlement there is little compensation for this cost as both types of animal are equally certain that their chosen habitat will continue to provide the resources they need (Palmer & Strathmann, 1981). No evidence exists in the literature to suggest that adult abalone reduce the suitability

of habitat for larvae or juveniles, indicating that the resources required by abalone larvae are as likely to be available locally as further afield. In addition, the kelp communities in which abalone are found are temporally stable (Dayton *et al.*, 1984; Tegner, in prep.). Thus the resources required by abalone are both uniformily available and temporally stable. As a consequence it should be expected that abalone will have evolved morphological and behavioural adaptations which will restrict larval dispersal.

For morphological reasons the primitive Archaeogastropoda cannot easily produce complex egg capsules nor undertake internal fertilization (Yonge, 1947). For this reason direct development benthic egg capsules (in which larvae pass through all development stages) and viviparity, the two most common means of restricting larval dispersion (Thorson, 1950; Mileikovsky, 1971), are not commonly found in Archaeogastropoda (Underwood, 1979). Underwood (1979) hypothesized that small gastropods denied these methods and pelagic larvae by their extremely small body size, would be forced to develop by non-dispersal lecithotrophy. Similarly it can be hypothesized that archaeogastropods such as haliotids, ecologically favoured by non-dispersal but morphologically constrained from evolving direct development or viviparity, are likely to develop this form of demersal development larvae.

Circumstantial evidence exists suggesting that abalone have behavioural adaptations which aid in restricting larval dispersal. For example, the only observation contained in the literature, of wide-scale spawning in haliotids in the natural environment, occurred in calm conditions and after several days of very calm weather (Breen & Adkins, 1980). From anecdotal information provided by commercial divers in Tasmania *H. rubra* also appears to spawn during calm weather. These observations suggest that abalone populations possibly select conditions of low water movement for spawning, adaptive behaviour which would minimize dispersion of gametes, eggs, and larvae. *H. rubra* maintains its gonads in a ripe state for long periods (Harrison & Grant, 1971; McShane *et al.*, 1986) as do many haliotids (see Mottett, 1978) and this may enable spawning to coincide with short irregular periods of low water movement. A similar phenomenon has been observed in the limpet *Cellana radians* in which spawning coincides with localized conditions of water movement (Creese & Ballantine, 1983), although for this limpet the required condition is high water movement. A number of haliotid species have been found to have variable spawning times (Newman, 1967; Poore, 1973; Shepherd & Laws, 1974; Shepherd *et al.*, 1985). More specifically several workers have observed abalone populations short distances apart spawning at different times (Webber & Giese, 1969; Hayashi, 1980); this has also been observed for *Haliotis rubra* (McShane *et al.*, 1986). These observations suggest that locally specific cues such as water movement, may be important in stimulating spawning in haliotids, which would explain why the rôle of more universal cues such as water temperature, and day length is so ambiguous (e.g. see Webber & Giese, 1969; Shepherd & Laws, 1974; Shepherd *et al.*, 1985; McShane *et al.*, 1986). This hypothesis is consistent with the results of the current study where spawning occurred between 18 and 29 September 1986. During this time there was a 3-day period (21–23 September) when winds were generally offshore and lighter

(2.3 $m \cdot s^{-1}$) than the average wind speed of September (7.6 $m \cdot s^{-1}$), a highly significant difference ($t = 9.17$; d.f. = 198; $P < 0.001$; Aust. Dept. Sci., unpubl. data). It is possible that the spawning of the abalone in the area studied coincided with this calm weather.

The eggs produced by haliotids are considerably heavier than water and if released over a boulder substratum, can be expected to sink and roll down into the substratum before hatching. Lodging the eggs within the substratum would prevent the eggs being rolled across sandy substrata away from reef habitat, and ensure that larvae begin their life in a habitat suitable for settlement. The behaviour observed by Breen & Adkins (1980) and supported by the observations of Quayle (1971), where spawning abalone climbed up onto kelp and prominent points of the substratum before releasing ova, is also reported by commercial divers for *H. rubra*. As abalone are often found on the edge of a rocky substratum and sand, where drifting kelp accumulates (Shepherd, 1973), this behaviour in calm water conditions may maximize the probability that eggs land on, and lodge in a hard substratum, rather than falling onto a sandy substratum.

Yano & Ogawa (1977) studied the behaviour of the larvae of *H. gigantea* under controlled laboratory conditions and found that the trochophore are positively phototactic and negatively geotatic. This study found that 75 h after hatching 80% of the larvae were still in the top 10 cm of the water column. Tegner & Butler (1985) used these results to imply that in the natural environment haliotid trocophores are generally positively phototactic and swim to the surface of the water where they remain for up to 75 h. This, however, conflicts with the results of Tanaka (1978), who while confirming that 3- and 5-day-old larvae (post fertilization) of the same species are positively phototactic, found them to be most abundant in the bottom layer of still water laboratory tanks. In the laboratory the trocophores of *H. rubra* swim freely for ≈ 10 h at 16 °C; they stop swimming and sink if they encounter hard surfaces or turbulence (J. Grant, pers. comm.; C. Sumner, pers. comm.). If this behaviour also occurs in the natural environment it is extremely uncertain as to whether the trocophore normally swim to the surface of the water. An alternative hypothesis is that being positively phototactic helps the larvae to orientate within the substratum. This could enable the larvae to move from deep within the substratum where the egg may have lodged towards the lighter upper boulder layers where suitable settlement sites (crustose corallines) are most abundant.

In addition to being consistent with the results of this experiment, the hypothesis that haliotid larvae are adapted to avoid dispersal, also offers an explanation for the observations of Breen & Adkins (1980) who found no abalone larvae, despite towing a plankton net over a known spawning site 2 and 3 days after the spawning. It also explains the findings of Tomita *et al.* (1977) who, by using a plankton pump, found small numbers of larvae in six of 19 samples. In only two of these samples were the larvae more numerous in the surface layer than the bottom layer and both these samples were taken from depths < 3 m. This hypothesis is also consistent with the observation reported in Sluczanowski (1984) that in an isolated substock a positive relationship had been found between the biomass of fecund abalone and the recruitment of 1^+ animals.

Restricted dispersal patterns for haliotid larvae are also consistent with the high levels of inbreeding observed in haliotid populations (Fujino, 1978; Fujio *et al.*, 1983).

The possibility that haliotid larvae generally avoid dispersal, rather than being pelagic and thus vagile, as at present assumed, has important implications for the management of abalone fisheries and deserves further consideration. Low dispersal rates would explain why many abalone fisheries have been so easily over-fished (Mottett, 1978). If larval dispersal is generally restricted, it is obvious that the potential for recolonizing areas which have been denuded of breeding stock by over-fishing, is extremely limited. The removal of small pockets of breeding stock would cause the overall productivity of a fishery to diminish, concentrating the fishing power of that industry on the remaining stocks, and making their collapse more likely.

ACKNOWLEDGEMENTS

We are grateful for the positive comment and criticism offered by Drs. R. W. Day and R. W. G. White, and Messrs. H. Williams and N. R. Loneragan, as well as the assistance provided by Prof. P. D. M. Macdonald. Our thanks also go to Mrs. E. Alexander for her assistance with the figures. This study was funded by the Fishing Industry Research Trust Account.

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