

Recruitment variation in sympatric populations of *Haliotis rubra* (Mollusca: Gastropoda) in southeast Australian waters

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ABSTRACT: Recruitment of abalone *Haliotis rubra* was examined in sympatric populations off southeastern Australia soon after the main spawning period. The size range of post-settlement juveniles (recruits) collected from the reef surface was indicative of recent settlement. Recruitment was strongest after the main spawning period but episodic minor recruitment in some populations was also observed throughout each year. Recruitment varied significantly both between populations and for each population over time; the latter varied over 3 orders of magnitude. The highest number of *H. rubra* recruits in a sample (the area contained within a 1 m² quadrat) was 12456. Abalone larvae can settle in densities much higher than has previously been assumed. Localised dispersal of larvae provides an explanation for our results. Variability in recruitment of *H. rubra* was high even when the density of the adult population was constant.

INTRODUCTION

Studies of benthic invertebrate communities in marine habitats have emphasized the importance of variations in recruitment in determining the distribution and abundance of adults (Denley & Underwood 1979, Underwood & Denley 1984, Caffey 1985, Connell 1985, Lewin 1986, Gaines & Roughgarden 1987). These studies have largely been concerned with intertidal species such as barnacles, but more recently an increasing emphasis on the early life history of benthic marine invertebrates has prompted investigation of other groups of invertebrates from subtidal habitats including sea urchins (Rowley 1989), holothuroids (Young & Chia 1982), ascidians (Davis 1987, 1988, Young 1989, Stoner 1990), corals (Gerrodette 1981), polychaetes (Hannan 1984, Butman 1987, 1989, Duggins et al. 1990); bryozoans (Yoshioka 1982, 1986, Keough 1983, 1986, Duggins et al. 1990), and gastropods (Fletcher 1987, McShane et al. 1988).

Although the studies cited above provide a clearer understanding of recruitment processes in populations of benthic invertebrates within a broad phylogenetic

framework, the sources of variation in recruitment for many species remain obscure. Only for those species with large larvae (some larvae of corals and ascidians) can dispersal and settlement be observed in situ (e.g. Gerrodette 1981, Davis 1988, Stoner 1990). Consequently conclusions drawn from such studies have been criticised as being unrepresentative of recruitment patterns in benthic species (e.g. Keough 1989) and may have little relevance for most taxa with microscopic pelagic larvae. Settlement patterns and the extent of larval dispersal of benthic marine invertebrates are most often inferred by observing recruitment – recruitment being the stage in the life history of a species when individuals are large enough to be observed. Often considerable time elapses between settlement and observations of recruits (Keough & Downes 1982). The repercussions of differential mortality can be such that recruitment may be unrelated to settlement (Keough & Downes 1982, Connell 1985, McGuinness & Davis 1989, McShane 1991a). A poor understanding of post-settlement mortality contributes to the unreliability of many studies of recruitment in marine benthic invertebrates (McGuinness & Davis 1989).

Haliotis rubra is a commercially exploited gastropod common on sublittoral reefs off southeastern Australia (Shepherd 1973, McShane et al. 1986, 1988). We show

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here that the measurement of recruitment in the abalone *H. rubra* shortly after settlement can provide information on factors influencing settlement and provide clues as to the source of recruitment variation.

MATERIALS AND METHODS

Location. We studied recruitment of *Haliotis rubra* populations off Mallacoota and Portland in southeastern Australia (Fig. 1). These populations were chosen because they are important commercially (McShane et al. 1986) and because they provided an opportunity to examine recruitment in differing habitats in disparate locations within the distributional range of the species. The regional physiographic characteristics off Mallacoota, including a description of the hydrodynamics, have been described by McShane et al. (1988) and Black & McShane (1990). Whereas populations of *H. rubra* at Mallacoota inhabit low relief basalt reefs, populations off Portland inhabit high relief limestone reefs in communities dominated by the kelp *Phyllospora comosa*. Moreover, the coast off Portland is often exposed to heavy southwest waves; the coast off Mallacoota is generally less exposed (Black & McShane 1990). Recruitment surveys at all locations were undertaken on the rocky substratum in a depth range of 6 to 10 m.

Recruitment. Surveys of *Haliotis rubra* recruits were undertaken on each of 6 occasions for each of 3 populations off Mallacoota; Sandpatch, Tullaburga Island and Bastion Point (during February, May, August and December 1987, December 1988, and January 1989). Sample sites were as described in McShane et al. (1988). Surveys of *H. rubra* recruits were also undertaken off Sandpatch during December 1989. Similar surveys were undertaken off Portland during December 1989 (Fig. 1).

At each site, 5 replicate 1 m² quadrats were randomly placed on the reef surface. Thus, areas of high prevalence of coralline algae were not targeted. However, surveys revealed that coralline cover on the reefs off Mallacoota and Portland ranged from 10 to 80 % (P. E. McShane unpubl.; see also McShane et al. 1988). In each quadrat, we used our venturi-suction method (McShane & Smith 1988) to sample recruits of *Haliotis rubra*. The method allows for collection of all post-settlement recruits (> ca 300 μ m) up to ca 12 mm in shell length. Larger individuals can be easily seen and collected by divers (McShane 1991a). The sorting of *H. rubra* from other biota and debris typically entrained in a sample was enhanced by the use of a 0.1 % solution of rhodamine B dye, which makes the tiny recruits more conspicuous (Hamilton 1969), and the separation method of Sellmer (1956) where ZnCl₂ is used to increase the specific gravity of a solution containing an epibenthic sample. Animals with a calcareous shell, such as *H. rubra* recruits, float when ZnCl₂ is added and can be separated from the other epibenthic material. Thus the mean sorting time per sample was reduced from 19 to 3 h. Recruits of *H. rubra* collected from each sample were counted and the shell length of each was measured to the nearest 10 μ m under a binocular microscope.

Population density. Population densities of *Haliotis rubra* were measured only off Mallacoota. Surveys in December of each year were used to estimate the density of adults. On each occasion at each location, divers collected all *H. rubra* in 3 randomly located transects consisting of 50 contiguous 1 m² quadrats as described by McShane et al. (1988). All *H. rubra* collected were counted and the shell length of each was measured to the nearest millimetre. Small cryptic individuals (< 20 mm) tend to be undersampled by searching but the method provides reasonable estimates of adult density (McShane et al. 1988, McShane 1991a).

RESULTS

The recruits of *Haliotis rubra* sampled in our surveys ranged in length from 320 to over 3000 μ m. Our length-frequency results can be used to estimate and compare

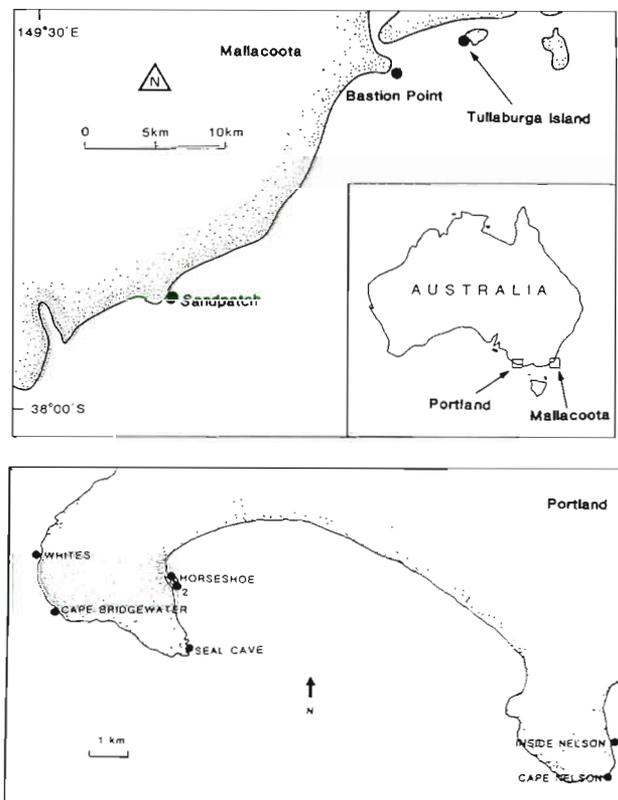


Fig. 1. Sample site locality

the timing and relative synchrony of settlement between populations. At settlement, an abalone larva is ca 350 μm in length (Ino 1952, McShane unpubl. data for *H. rubra*). Data from Garland et al. (1985) indicate the post-settlement growth rate of *H. rubra* to be ca 10 $\mu\text{m d}^{-1}$. Thus the length of the smaller recruits sampled in our study was indicative of recent settlement.

Mallacoota

Analysis of variance indicated that the mean density of recruits was similar between sites at each of the 3 locations, Sandpatch, Tullaburga Island and Bastion Point ($p > 0.2$). An exception was for *Haliotis rubra* recruits sampled from Tullaburga Island during December 1988 where there was a significant difference in density between sites ($F_{1,8} = 7.4, p = 0.03$). Data were pooled in all other cases for comparison of recruitment between populations and over time by 2-way ANOVA.

During 1987, when samples were taken throughout the year, recruits were present on each occasion for each of the 3 populations Sandpatch, Tullaburga Island and Bastion Point (Fig. 2). However, in general the length-frequency results indicated that there was only one main period of recruitment extending over December and January. An exception was for the population at Bastion Point where substantial recruitment occurred during May (a distinct mode of recently settled individuals was apparent; mean density \pm SE: $93 \pm 47 \text{ m}^{-2}$, mean length $450 \pm 32 \mu\text{m}$) and minor recruitment was observed in August (mean density \pm SE: $5 \pm 3 \text{ m}^{-2}$, mean length $1.1 \pm 0.6 \text{ mm}$; Fig. 2).

The mean lengths of recruits sampled in December were generally less than those of recruits sampled in

January (Fig. 3); a result consistent with a December spawning and settlement for *Haliotis rubra*. However, recruits sampled off Sandpatch in December 1989 had a significantly greater mean shell length than that of recruits collected in December of previous years (by ANOVA, $F_{2,432} = 3.2, p < 0.001$). The mean length of recruits sampled in December 1987 and 1988 was indicative of a post-settlement age of ca 10 d. In contrast, the length distribution of recruits sampled during December 1989 (Sandpatch) indicates that settlement started as early as October that year.

Analyses of variance revealed that the mean length of *Haliotis rubra* recruits for the 3 populations off Mallacoota was similar for samples collected during December 1987 ($F_{2,467} = 0.2, p = 0.15$) but differed for samples collected during December 1988 (mean length $F_{2,523} = 4.2, p < 0.001$). Fig. 4 shows that mean lengths for recruits (1988 samples) from Sandpatch and Tullaburga Island are similar and greater than those at Bastion Point.

If the post-settlement growth rates are similar between populations, the difference in shell length of recruits sampled during December 1988 suggests that settlement of *Haliotis rubra* in the Bastion Point population occurred about 10 d after settlement at Sandpatch or Tullaburga Island. The mean length of recruits sampled in January 1989 from Bastion Point ($440 \mu\text{m}$) suggests a post-settlement age of about 9 d.

Densities of *Haliotis rubra* recruits in our samples varied from 0 to 12456 m^{-2} . The mean density of recruits sampled off Bastion Point during December 1988 was 1860 m^{-2} and is orders of magnitude higher than estimates from comparable studies of abalone, for example Prince & Ford (1985) (0 to 15 m^{-2}), Shepherd & Turner (1985) (up to 13 h^{-1} searching time), but comparable with estimates of recruitment by Tanaka et al. (1986).

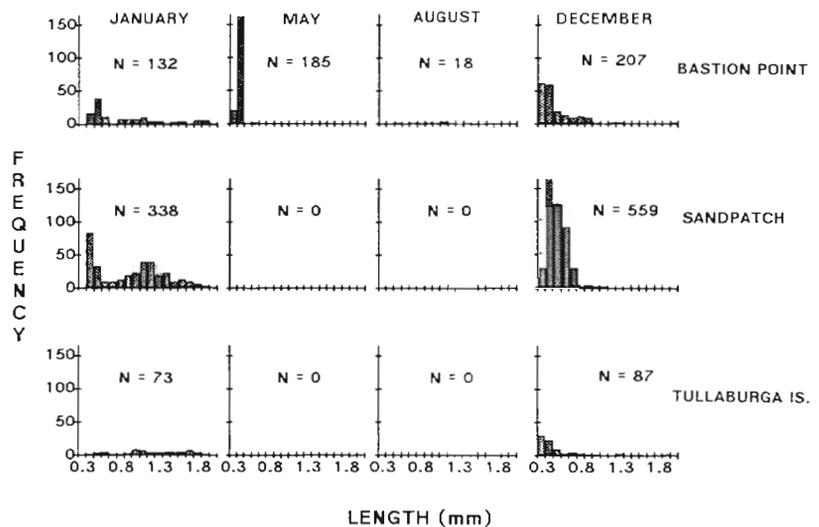


Fig. 2. *Haliotis rubra*. Length-frequency distributions of recruits sampled during 1987 in 3 populations: Bastion Point, Sandpatch, and Tullaburga Island

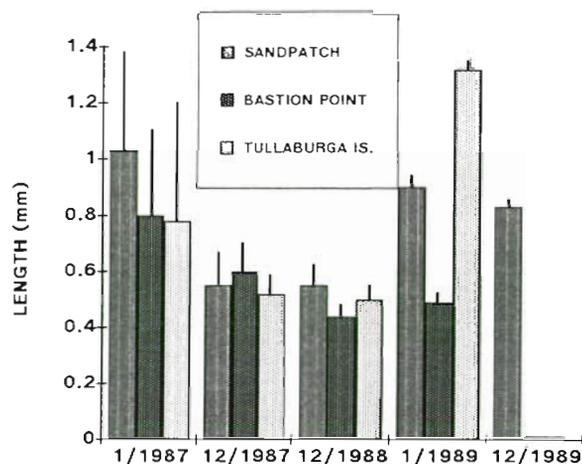


Fig. 3. *Haliotis rubra*. Mean shell length of recruits sampled on 5 occasions from 3 populations: Sandpatch, Tullaburga Island and Bastion Point. Vertical bars represent standard errors

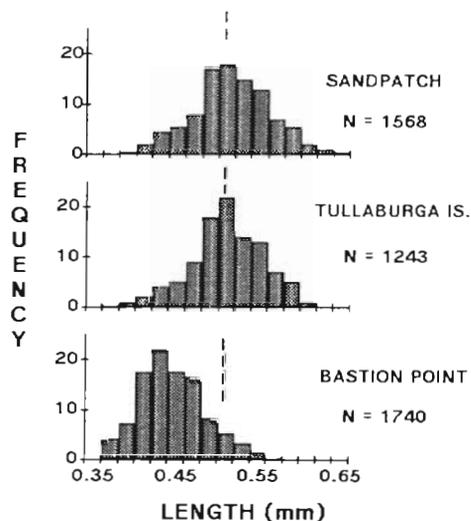


Fig. 4. *Haliotis rubra*. Length-frequency distributions of recruits from 3 populations: Sandpatch, Tullaburga Island and Bastion Point, sampled during December 1988. Dashed line indicates median frequencies for the Sandpatch and Tullaburga Island populations

A comparison of recruitment of *Haliotis rubra* in December (the main spawning period) with a 2-way analysis of variance revealed that the density of recruits varied between years but not between populations (Table 1); estimated densities of recruits in 1988 at Bastion Point and Sandpatch were 2 orders of magnitude greater than that recorded in December 1987. The variability of recruitment within a population was high; replicate counts at one site at Sandpatch ranged from 769 to over 12456 recruits m^{-2} . Such spatial variation in recruitment within a population made identification of between-population variation tenuous.

Table 1. *Haliotis rubra*. Recruitment variation in 3 populations off Mallacoota. Data are densities (m^{-2}) measured in December 1987 and 1988 and are means \pm SE

| Population | 1987 | 1988 | | | |
|-----------------------------|--------------------|----------------|--------------------|------|-------|
| Sandpatch | 54.2 \pm 18.1 | 1705 \pm 796 | | | |
| Tullaburga Island | 6.9 \pm 1.9 | 171 \pm 61 | | | |
| Bastion Point | 22.6 \pm 5.2 | 1860 \pm 431 | | | |
| Analysis of variance | | | | | |
| Source of variation | SS | df | MS | F | p |
| Population | 1.03 $\times 10^7$ | 2 | 5.17 $\times 10^6$ | 2.10 | 0.131 |
| Year | 2.40 $\times 10^7$ | 1 | 2.40 $\times 10^7$ | 9.77 | 0.003 |
| Interaction | 9.57 $\times 10^6$ | 2 | 2.79 $\times 10^6$ | 1.95 | 0.152 |
| Error | 1.50 $\times 10^8$ | 61 | 2.46 $\times 10^6$ | | |

Portland

Analysis of variance indicated that the mean density of *Haliotis rubra* recruits was similar between sites at each of the 7 locations surveyed off Portland (ANOVA, $p > 0.28$). Data from individual sites were therefore pooled for comparison of recruitment between populations. Analysis of variance revealed that recruitment varied between populations ($F_{6,28} = 3.4$, $p = 0.013$; Fig. 5). Mean densities of recruits were comparable with estimates derived from Sandpatch (off Mallacoota) during December 1989 ($9.1 \pm 0.5 m^{-2}$); mean densities off Portland ranged from 7.2 to $163.4 m^{-2}$.

Length-frequency data indicated a size range similar to that for the Mallacoota populations; recruits varied in length from 390 to 2890 μm . However, in general, the length-frequency distributions of the 7 populations sampled were negatively skewed with most recruits ranging in length from 400 to 700 μm (Fig. 6); a size range indicative of recent settlement. Analysis of variance revealed that mean lengths of recruits varied between populations ($F_{6,1512} = 4.3$, $p < 0.001$). A pairwise comparison of means by Tukey's HSD test showed that recruits from Cape Bridgewater were smaller than those from Whites Beach and Seal Caves which had similar means (Fig. 6).

The size composition of recruits differed even between neighbouring populations. The length-frequency distribution of recruits from Cape Nelson was unimodal (mean length 655 μm) whereas a mode of larger recruits was apparent in the distribution of recruits from Inside Nelson (median length 1670 μm ; Fig. 7). A comparison of the 2 populations at Horse-shoe, separated by about 100 m, revealed that the mean length (\pm SD) of recruits was significantly different ($1.15 \pm 0.48 mm$; $1.49 \pm 0.66 mm$; ANOVA, $F_{1,191} =$

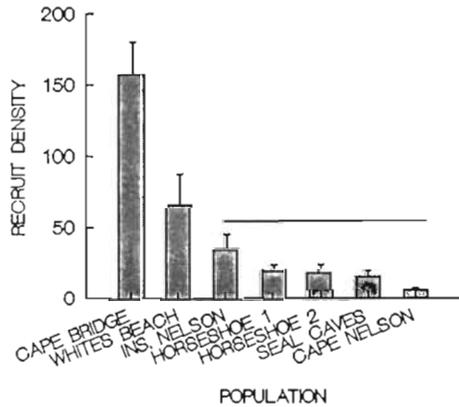


Fig. 5. *Haliotis rubra*. Comparison of the density of recruits sampled from 7 populations off Portland. Data are means (recruits m^{-2} , $N = 5$). Vertical bars indicate standard errors for each population. Horizontal bars indicate populations with similar densities (Tukeys HSD test, $p > 0.05$)

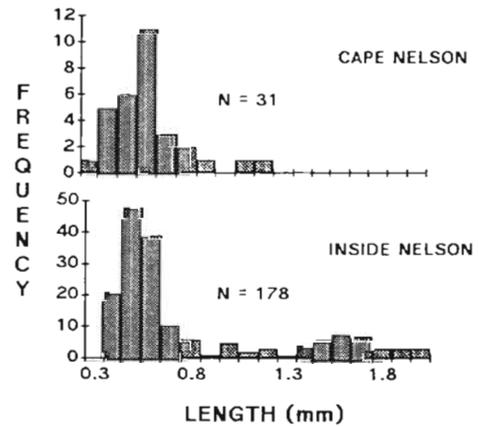


Fig. 7. *Haliotis rubra*. Comparison of the length-frequency distribution of recruits sampled from 2 neighbouring populations, Cape Nelson and Inside Nelson

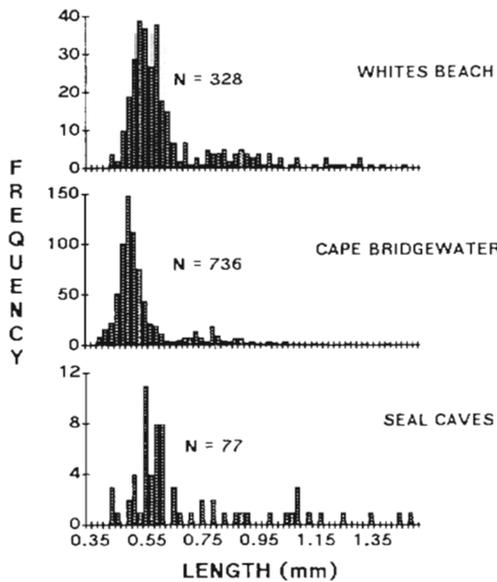


Fig. 6. *Haliotis rubra*. Length-frequency distribution of recruits sampled from 3 neighbouring populations off Portland: Whites Beach, Cape Bridgewater and Seal Caves

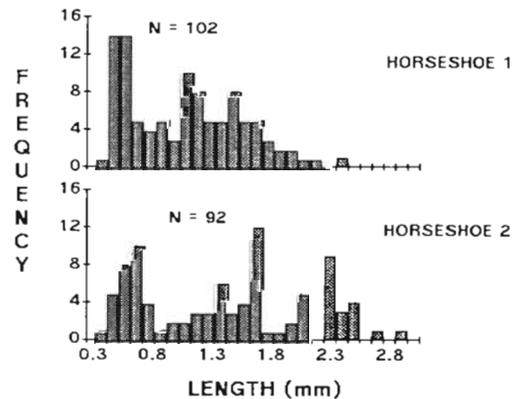


Fig. 8. *Haliotis rubra*. Comparison of the length-frequency distribution of recruits sampled from 2 neighbouring populations, Horseshoe 1 and Horseshoe 2

20.0, $p < 0.01$). Fig. 8 shows a mode of larger recruits at Horseshoe 2 (median length 2370 μm) which were infrequent at Horseshoe 1.

Adult density

The relative density of adult *Haliotis rubra* in the 3 populations off Mallacoota were different (means for Sandpatch and Tullaburga Island were similar, ANOVA, $p > 0.1$) but were similar from year to year for each population (ANOVA, $p > 0.6$). Mean densities (ind. $m^{-2} \pm SE$) of adults were 3.5 ± 1.5 for Sandpatch,

3.4 ± 1.4 for Tullaburga Island and 2.5 ± 0.8 for Bastion Point. Thus, for each population, recruitment varied independently of adult density; there was no evidence of a stock-recruitment relationship ($N = 7$, $r = 0.13$, $p = 0.85$).

DISCUSSION

Our surveys show that recruits of *Haliotis rubra* can be censused soon after settlement; the size of many of the recruits approximated that estimated for metamorphosed larvae of other species of abalone (Ino 1952, Ebert & Houk 1984). The results also suggest that settlement of *H. rubra* can be dense and episodic; densities of recruits were much higher than those previously reported (Prince & Ford 1985, Prince et al. 1987) for the species and were comparable to the densities of opportunistic colonizers, such as barnacles, which colonize hard substrata (Denley & Underwood 1979, Caffey 1985, Connell 1985, Gaines et al. 1985). These findings

together with our observations of spatial variability in recruitment of *H. rubra* can be explained by the localized dispersal of larvae (Prince et al. 1987, McShane et al. 1988) as discussed below. Another important finding of our study is that the variation in recruitment was high at constant adult population size.

The density of recruits that we recorded for some populations is consistent with larval 'swarms' remaining close to the habitat of parents but is contrary to statements that abalone larvae are absent near the time of spawning (Breen & Adkins 1980; see also McShane 1991b). However, abalone larvae are difficult to detect because they are episodically released, relatively short-lived and may be expected to be diffused and dispersed to low concentrations in the open sea (Strathmann 1985, McShane et al. 1988). Larval 'swarms' of passively transported larvae can only exist if retained in eddies or if water currents are sufficiently attenuated such that diffusion and dispersal are minimized (McShane et al. 1988, McShane 1991b).

The most striking result of our study was the large interannual and spatial variation in recruitment of *Haliotis rubra*. This finding parallels results from studies of other subtidal benthic invertebrates (e.g. Keough & Downes 1982, Keough 1983, Caffey 1985, Connell 1985, Yoshioka 1986, Fletcher 1987). At Sandpatch, an easterly flowing current forms an eddy on the eastern side of the headland where recruits are concentrated (McShane 1991b); eddies can entrain larvae (Black 1990). At Portland, 2 neighbouring populations of *H. rubra*, Cape Nelson and Inside Nelson, are hydrodynamically isolated; the population at Inside Nelson inhabits a sheltered reef in the lee of an exposed headland (Cape Nelson). Recruits were more dense at the sheltered location, where larvae are more likely to be entrained (McShane et al. 1988), than at Cape Nelson which is subject to the prevailing south-westerly waves. In addition Cape Nelson had fewer kelp beds than the other locations at Portland (P. E. McShane unpubl.). Kelp stands are important in trapping larvae and localising recruitment (Eckman et al. 1989, Duggins et al. 1990), and dense stands of the kelp *Phyllospora comosa* at Whites Beach and Cape Bridgewater can be expected to entrain larvae. At Horseshoe, a sheltered location, neighbouring populations of *H. rubra* differed in the size composition of recruits. In such an environment, with dense kelp beds and mild water movement, neighbouring populations may be expected to be hydrodynamically isolated resulting in little exchange of larvae. For these reasons we also expected relatively dense settlement at Horseshoe but the relatively large size of the recruits at Horseshoe suggested that settlement had occurred at least a month prior to settlement in the other Portland populations and the recruitment

observed would be substantially less than the actual settlement.

The high variability in recruitment of *Haliotis rubra* may reflect variability in larval abundance, a phenomenon recorded for other species of marine invertebrates (Keough 1983, Gaines et al. 1985, Yoshioka 1986, Gotelli 1987), but, because detection of abalone larvae in their natural habitat is so difficult, this hypothesis has not been tested. Nonetheless, our studies of several *H. rubra* populations near Mallacoota showed that recruitment was regional rather than local. Thus there were 'good' and 'bad' years for recruitment; recruitment was generally high in 1988 and low in 1987 indicating year-to-year variation in exogenous factors.

The size composition of recruits suggested that settlement was episodic and asynchronous between populations. The presence of larger 'modes' of recruits in some populations, for example Horseshoe, and the presence of recruits outside the 'normal' spawning time at Bastion Point indicated that *Haliotis rubra* settle unpredictably and that settlement was not uniform even between neighbouring populations. Local dispersal of larvae provides an explanation of these results. As an alternate explanation, differences in rates of growth and survival of recruits between populations may have caused the apparent differences in the size composition of recruits between populations. While we cannot reject this latter hypothesis there is little evidence to support it. At Horseshoe, a sheltered site, the 2 populations studied inhabited the same reef complex. Many of the populations of *H. rubra* at Portland were in close proximity and occupied similar habitat. There was no evidence of major differences in community composition, including likely predators, nor was there any evidence of differences in the physiography of the reef which could explain differential survival. At Mallacoota, the 3 populations of *H. rubra* studied were part of similar communities inhabiting reefs similar in depth and topography (McShane et al. 1988).

A stock-recruitment relationship (cf. Ricker 1954, Beverton & Holt 1957) is an attractive hypothesis to explain variation in recruitment in abalone. McShane et al. (1988) and Prince et al. (1988) showed that recruitment of *Haliotis rubra* correlated with adult abundance; yet our results show that recruitment within a single population varied enormously from year to year with constant adult abundance. In contrast, Prince et al. (1988), on the basis of results from surveys of several populations, claim a stock-recruitment relationship for *H. rubra*; however they surveyed recruits at least 2 mo after settlement and combined data collected at different times from different populations. The variation in recruitment of benthic invertebrates in general is so high (Yoshioka 1986) that correlations with the abundance of spawning stock are tenuous.

Not surprisingly stock-recruitment relationships are seldom evident in benthic invertebrate populations (Hancock 1973).

The evidence suggests that events in the early life history are as important in determining the population structure of *Haliotis rubra* as they are in other species of benthic marine invertebrates. Recruitment varies stochastically. Factors controlling spawning periodicity could contribute to such variation; both aspects would be worthy of further study.

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