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RELATIONSHIPS BETWEEN RECRUITS OF ABALONE *HALIOTIS MIDAE*, ENCRUSTING CORALLINES AND THE SEA URCHIN *PARECHINUS ANGULOSUS*

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In kelp beds of the South-Western Cape, South Africa, a strong positive relationship exists between the sea urchin *Parechinus angulosus* and juveniles of the abalone *Haliotis midae*. Field surveys reported here revealed a positive, but weak, association between this urchin and *H. midae* recruits (i.e. individuals <3 mm shell length). Selectivity indices showed that recruits occurred exclusively on encrusting coralline algae and showed preferences for strongly textured corallines, rather than those with smooth texture. On smooth corallines, around 80% of recruits were under urchins, compared with about 25% on textured corallines, suggesting that any need for shelter beneath urchins is greatest on smooth surfaces.

Encrusting corallines have long been implicated in the settlement of abalone larvae (Crofts 1929, cited in Shepherd and Daume 1996, Morse *et al*. 1979, Morse and Morse 1984). Saito (1981), Garland *et al*. (1985), Shepherd and Turner (1985), Prince *et al*. (1988) and Tarr *et al*. (1996) have also highlighted the association between corallines and abalone post-larvae. During the early post-larval stage, while abalone are associated with encrusting corallines, they are camouflaged to match the pink or off-white colour of the corallines, and can be further recognized by their small size (<3 mm) and the possession of a single shell whorl. The term "recruit" is used here to distinguish this stage of the life cycle from the subsequent "juvenile" phase, when the abalone become photophobic, move into cryptic habitats and assume a different colour.

One factor of central importance to the survival of these early recruits is the specific coralline microhabitat they occupy after settling. Within the gross grouping of "crustose corallines", there exists a wide diversity of morphological forms, and attention has recently been focused on the potential effects of micro-scale differences in coralline morphology on the survival of abalone recruits. Several such effects have been mooted, one being the differential accumulation of diatom and bacterial food sources (Shepherd and Turner 1985, Matthews and Cook 1995, Kawamura et al. 1995). Shepherd and Daume (1996) report unpublished observations that high densities of grazing chitons and gastropods tend to occur on smooth, even substrata, and that their lower densities on irregular corallines lead to accumulation of the biofilms consumed by abalone recruits. Bulldozing by larger grazers may also kill recruits (Andrew and Underwood 1992). Again, the morphology of the substratum might influence vulnerability of recruits to grazing. Conversely, however, grazers may prevent epiphytic fouling and overgrowth of corallines (e.g. Breen and Mann 1976, Fletcher 1987, Vadas and Steneck 1995), so maintaining a substratum suitable for settlement of abalone larvae (Tegner and Levin 1982). Several species of urchins have specifically been shown to fulfil this role (Lawrence 1975, Breen and Mann 1976, Vadas and Steneck 1995), sometimes even creating monocultures of coralline algae, often termed "barren grounds" (Fletcher 1987, Andrew 1989).

In kelp beds of South Africa's South-Western Cape, a strong relationship exists between juvenile abalone *Haliotis midae* and the local sea urchin *Parechinus angulosus* (Tarr *et al*. 1996), and both occur almost exclusively on encrusting coralline algae (Day and Branch 2000). Concealment of juvenile *H. midae* beneath urchins probably grants them protection against predators. In contrast, given that abalone recruits are cryptic on corallines and do not exhibit the photophobic responses typical of juveniles (Tegner and Butler 1989, McShane 1992, current authors' pers. obs.), it is intuitively less likely that urchins play a comparable role in protecting recruits.

What is the likelihood of an association between *P. angulosus* and recruits of *H. midae*, and does the morphology of different types of corallines affect the distribution of abalone recruits and their relationship with urchins? To explore these questions, field observations were used to investigate (1) the distribution patterns of recruits in relation to coralline morphology and (2) the existence of any relationship between these recruits and sea urchins.

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MATERIAL AND METHODS

Site

At six sites on the eastern shores of the Cape Peninsula, preliminary surveys of abalone recruits were undertaken at depths of 1–3 m, over the period of peak recruitment, i.e. November–February (Newman 1967). Only one site, Miller's Point in False Bay (34°15′S, 18°28′E), yielded sufficient numbers of recruits for quantitative analyses. This site was therefore selected for the intensive surveys reported here.

Pilot study

A pilot study was conducted at Miller's Point, to determine substrata never occupied by recruits. Two divers spent 30 minutes searching each habitat considered "marginal", i.e. sand, crevices, foliar algae, the undersides of rocks, sponges, colonies of compound ascidians, and hard surfaces overlain by fine sediments. Because recruits were not found on any of those substrata, the subsequent intensive survey focused on those substrata that did support recruits, i.e. exposed, clean, rocky substrata that were either bare or covered by encrusting algae.

Surveys of substratum availability and recruit abundance

The proportions of different substrata constituting the exposed hard surfaces of the shallow subtidal region were determined from 80 quadrats (0.25 m^2) placed haphazardly on rocky surfaces. If more than 20% of the area of a quadrat consisted of "marginal" substrata, the quadrat was moved to a new position. For each quadrat, the percentage cover of each species of encrusting coralline was recorded, as well as that of bare rock, the encrusting alga *Hildenbrandia lecanellierii*, colonial ascidians, sponge and sediment. Percentage cover was estimated visually by pairs of divers and the average of their two estimates used. This approach has been shown to be more accurate than using point-intercept counts on quadrat grids (Dethier *et al*. 1993).

Smaller quadrats (0.0625 m^2) were used for the recruit survey, which was conducted in the same area. In all, 87 quadrats were placed haphazardly on hard substrata, and the numbers of recruits on each type of substratum were recorded. Urchins found in the quadrats were lifted and a count was made of any recruits concealed beneath them.

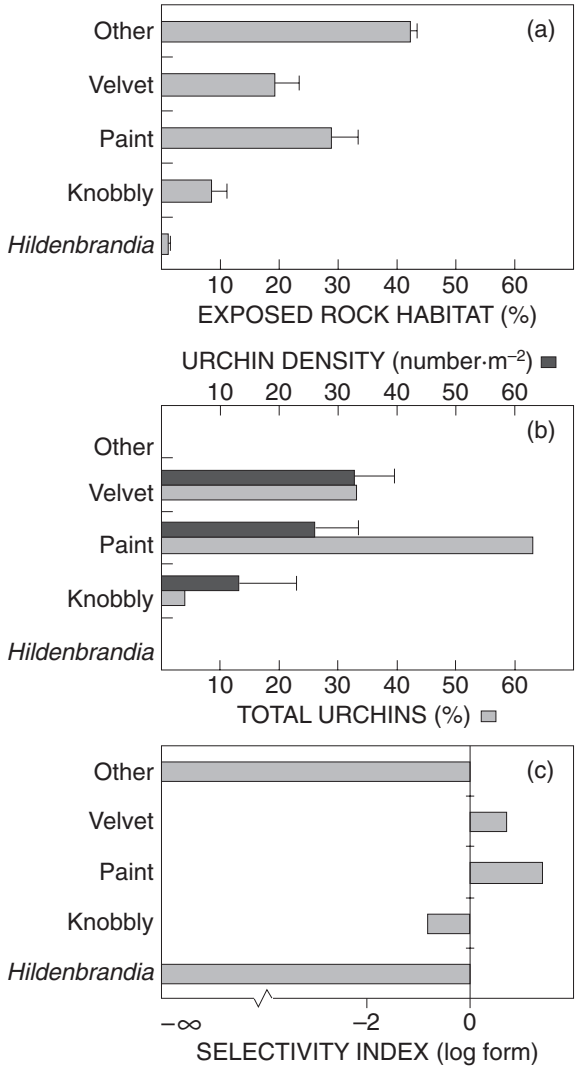

Fig. 1: Selection of substrata by urchins – (a) percentage of different types of substrata, (b) mean urchin densities and proportional abundance (%) of urchins on different substrata, and (c) selectivity indices of urchins for each category of substratum. Negative values indicate rejection or avoidance and positive ones show preferences for a particular substratum. Error bars denote +1*SD*

Data analysis

Substrata were grouped into broad textural categories, namely: bare rock, sponge, compound ascidians, *Hildenbrandia*, "paint" coralline (very thin encrusting coral-

lines that assume the texture of the underlying surface, and were dominated by *Leptophytum ascervatum*), "knobbly" corallines (slightly thicker crusts, with knobbly bumps across the surface, consisting of *L. foveatum*, *L. discrepans* and *Spongites discordias*), and "velvet" corallines (thick, smooth crusts, consisting almost entirely of *Heydrichia woelkerlingii*). The categories of corallines employed correspond to those of Woelkerling *et al*. (1993) as follows: knobbly = "lumpy" and "warty", velvet = "thick, smooth", paint = "thin, uneven".

The mean percentage cover of each category of substratum was calculated and urchin counts were converted to densities per m^2 of each substratum. Recruit data were converted into densities per category of substratum in the same manner. The total numbers of recruits on each substratum (based on pooled quadrat data), the proportion of these recruits found under urchins, and the percentage of recruits found on each type of substratum were all calculated.

A selectivity index (Gabriel 1978), based on the relationship between substratum availability and proportional abundance of animals on each substratum, was used to assess whether urchins or recruits displayed any selection (or avoidance) of particular substrata. In logarithmic form, the index (W) yields values from $-\infty$ (negative selection) to $+\infty$ (positive selection), with values of 0 indicating random selection,

$$W = p1q2/p2q1 \quad ,$$

where $p1$ = % of urchins or recruits occupying a particular substratum; $p2$ = % of area covered by that particular substratum; $q1 = (100-p1)$; $q2 = (100-p2)$.

The area of each substratum covered by urchins was calculated from the mean radius of the urchins (35 mm, including spine canopy) and the density of urchins found on each type of substratum. The proportions of recruits found under urchins were plotted against the proportions of each substratum occupied by urchins. The data were then compared graphically to a hypothetical 1:1 line, indicating an absence of any selectivity by recruits for urchins (as amplified in the Results). A χ^2 test was used to determine whether the data departed significantly from this line of "no selectivity".

RESULTS

Urchins and corallines

Of the encrusting algal substrata, paint corallines occupied the greatest surface area, followed by velvet corallines, knobbly corallines and, finally, relatively small areas of *Hildenbrandia* (Fig. 1a). Areas of substrata classed as "other" (i.e. sediment, foliar algae, sponges and compound ascidians), collectively constituted almost 50% of the cover, but individually never approached the contributions of the three types of corallines. Areas of bare rock occupied <1%.

Densities of urchins (Fig. 1b) were slightly higher on velvet corallines than on paint corallines, and both exceeded those on knobbly corallines. No urchins were found on *Hildenbrandia* or any of the "other" substrata. Over the entire area, however, a far higher proportion of urchins was found on paint corallines than any other substratum, reflecting the higher total availability of this substratum.

The selectivity indices (Fig. 1c) show that the strongest positive selection displayed by urchins was for paint corallines, followed by velvet corallines. Slightly negative selection was displayed for knobbly corallines; *Hildenbrandia* and "other" substrata were always avoided.

Recruits and corallines

No abalone recruits were ever found on *Hildenbrandia* or "other" substrata; total densities were highest on knobbly corallines, intermediate on paint and lowest on velvet corallines (Fig. 2a). The proportions of recruits found under urchins were far greater when they occurred on velvet corallines (80%) than on paint (31%) or knobbly corallines (24%).

Figure 2b shows the proportions of recruits on each substratum. These can again be compared with the availability of each type of substratum (Fig. 1a). Selectivity indices (Fig. 2c) indicated strongest positive selection by recruits for knobbly corallines, followed by paint corallines. Weak, negative selection was displayed for velvet corallines. Selection for *Hildenbrandia* and "other" substrata was strongly negative, confirming the pilot study, which showed a total absence of recruits from those substrata grouped as "other".

Recruits and urchins

For each of the three coralline types, the percentages of recruits found beneath urchins were related to the proportions of substratum area occupied by urchins (Fig. 3a). Data points not departing significantly from the hypothetical line showing a 1:1 relationship between these two proportions would indicate no real preference by recruits for urchins. For example, if 5% of the substratum were to be covered by urchins, then purely by chance one would expect 5% of the

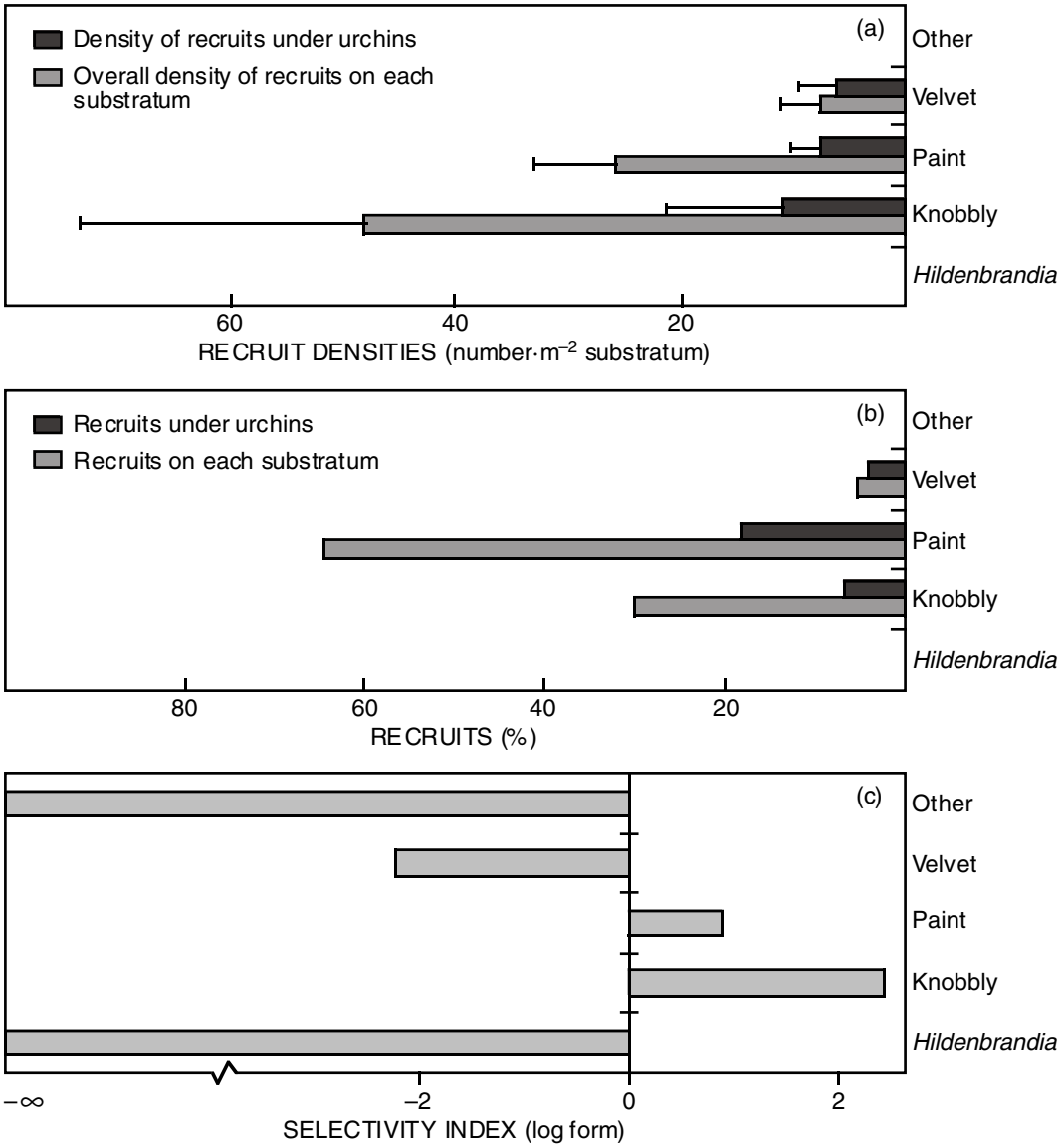

Fig. 2: Selectivity of substrata by abalone recruits – (a) overall densities of recruits found on each substratum and mean densities of those found beneath urchins, (b) proportional occupation of different substrata by abalone recruits, and (c) selectivity indices of recruits for each category of substratum. Negative values indicate rejection or avoidance and positive values show preferences for a particular substratum. Error bars denote +1*SD*

recruits to be found beneath urchins. The actual data fell significantly above this line (χ^2 tests, $p < 0.001$ in all cases), indicating positive selectivity for the urchins. This selectivity for urchins was, however, far stronger in the case of recruits on velvet corallines than for those on either knobbly or paint corallines.

A previous analysis has shown very strong selectivity of urchins by juveniles of *H. midae*, with >97%

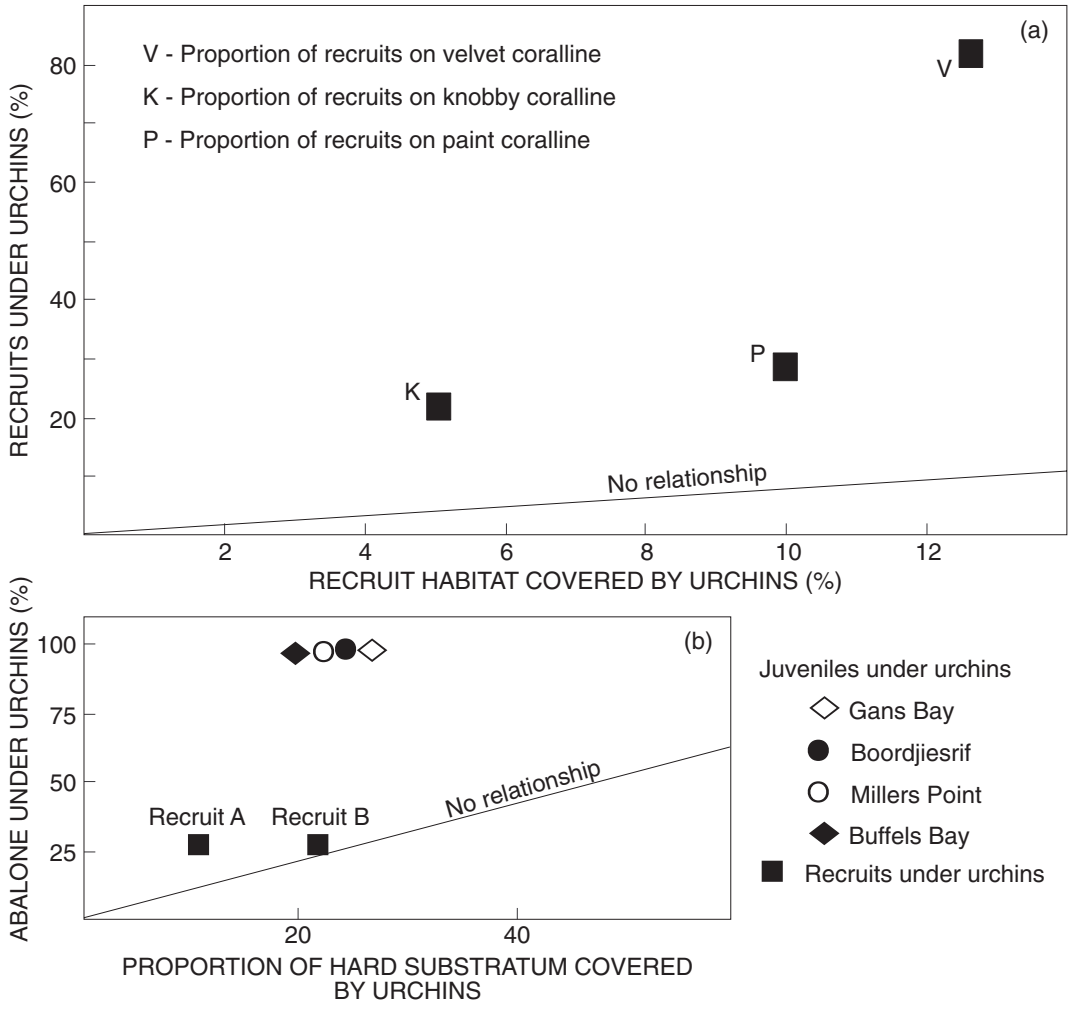

Fig. 3: Relationships between abalone recruits and urchins, compared with those between abalone juveniles and urchins – (a) relationship between the areas of particular types of corallines covered by urchins, and the proportion of abalone recruits found beneath urchins, within each coralline category, and (b) comparison of the same relationship, after pooling the data for recruits from different coralline categories. Data for juvenile abalone are for four sites on Cape Peninsula, and are taken from Day and Branch (2000). The plotted lines in both (a) and (b) show a hypothetical 1:1 relationship; data that do not depart significantly from these lines indicate an absence of any relationship between abalone and urchins. "Recruit A" = relationship when only the proportions of urchins found on corallines are considered. "Recruit B" = relationship when the proportions of urchins on all hard substrata are considered, so making the data equivalent to those for juvenile abalone

of the juveniles being found beneath urchins, even though the latter covered only 20–28% of the substratum (Day and Branch 2000). In the case of recruits, however, the manner in which the data were gathered differs in two respects from that for juveniles. First, the data for recruits relate to three different categories of corallines, whereas those for juveniles deal with encrusting corallines as a group. Second, the analysis of recruits excluded crevices, because the pilot study showed that these were not a potential habitat for recruits. The data for juveniles included this habitat. To allow direct comparison between these two sets of

data, the information for recruits was converted in two steps. First, the data were pooled across the different substrata (see "Recruit A" in Fig. 3b). A χ^2 analysis of these pooled data showed that recruits on corallines occurred under urchins more frequently than would be expected by chance ($df = 1$, $p < 0.001$).

As a second step, these data were then converted to include crevices among the available habitats, allowing a direct comparison of juvenile and recruit associations with urchins. The result ("Recruit B" in Fig. 3b) shows that the recruits do not differ significantly from the hypothetical 1:1 line ($df = 1$, $p > 0.05$), thus indicating that there is no more than a chance relationship between recruits and urchins.

Therefore, when the entire reef (including crevices) is considered, recruits showed no selectivity for urchins. Only within the confines of coralline habitats (admittedly the preferred habitat of recruits) did they display any selectivity for urchins, and even this is weak when compared with that shown by juveniles (Fig. 3b).

DISCUSSION

Fricke (1979) found urchin distributions in False Bay to be directly related to the availability of hard substrata, and the current pilot surveys showed that these are the only substrata of relevance to the distribution of abalone recruits. The absence of urchins and recruits from stands of *Hildenbrandia* and the other non-coralline substrata (Fig. 2) is not surprising. Shepherd (1973) has already shown that urchins do not favour sponge as a substratum, and Tegner and Butler (1989) noted that abalone recruits prefer clean, sediment-free substrata.

Encrusting corallines therefore appear to be as important for *H. midae* recruits as they are for other *Haliotis* species. Differences in the selectivity of *H. midae* recruits for different types of corallines do, however, exist. Recruits appear to favour (or survive longest on) strongly textured knobbly corallines, and this selectivity may entail several advantages. One possibility is reduced predation. The principal predators of abalone recruits are probably nematodes and polychaete worms (McShane 1992), which inhabit the thick crusts of velvet corallines more abundantly than they do the thinner knobbly and paint corallines (Keats *et al.* 1994). Knobbly corallines may also provide better shelter from water sheer (McShane 1991, 1992, McShane and Naylor 1995), retain higher densities of diatoms and bacteria because larger grazers favour smoother substrata (Steneck and Paine 1986, Shepherd and Daume 1996), and provide protection against the bulldozing and grazing activities of larger grazers known to ingest abalone recruits incidentally (Fletcher 1987, Andrew and Underwood 1992). In the area investigated here, *P. angulosus* exhibited no signs of being an active grazer, rather being sedentary and trapping drift kelp (Day 1998, Day and Branch in prep.). It is therefore unlikely to constitute a threat to abalone recruits. The same is, however, not true for other grazers that are present, such as the winkles *Turbo* spp. and *Oxystele* spp., and knobbly corallines may protect abalone recruits against such grazers. It should, however, be noted that Shepherd and Daume (1996) found that extremely lumpy surfaces are not favoured by abalone recruits, and argued that such forms are too irregular for adequate pedal adhesion.

All the above possible reasons why particular corallines may benefit *H. midae* recruits must remain speculative, because the correlative field data presented here cannot distinguish among them. There is nonetheless a clear-cut preference by recruits for encrusting corallines over other substrata, and for knobbly and paint corallines over velvet corallines. These results need to be tested elsewhere to explore their generality, particularly in view of the hitherto generally held belief that velvet corallines are the preferred substratum of recruits of *H. midae* – a belief so strong that monitoring of recruitment has been based on surveys of velvet corallines alone (R. J. Q. Tarr, Marine & Coastal Management, pers. comm.). Other areas may have different species of crustose corallines, and abalone recruits may respond differently to them even if they have equivalent textures.

The relationship between recruits and urchins is considerably different from that between juveniles and urchins (Fig. 3). Recruits do exhibit a preference for urchins, particularly if they occur on velvet corallines that probably provide less protection than other more textured corallines. However, their relationship with urchins is nothing like as strong as that shown by juvenile abalone, almost all of which are found under urchins (Day and Branch 2000). This difference is not really surprising. As long as recruits are cryptic on their coralline substrata, and particularly if they are protected by surface irregularities, there are no obvious benefits to be derived from sheltering beneath urchins. Initial habitat selection by recruits seems to be for corallines; selection for urchin cover is relatively weak and acts only within the confines of the preselected coralline substrata. Recruits found under urchins show no behavioural response if the urchin is removed, and remain *in situ*. By contrast, juvenile abalone deprived of their urchins immediately seek shelter and soon locate and hide beneath other urchins (Day 1998).

Despite the weak direct links between sea urchins and abalone recruits, indirect links may exist. Experimental removal of *P. angulosus* leads to the virtual disappearance of both recruits and juveniles of *H. midae* (Day 1998, Day and Branch in prep.). Numerous studies have shown that grazing urchins play an essential part in the maintenance, and even the creation, of crustose coralline stands (Breen and Mann 1976, Tegner and Levin 1982, Fletcher 1987, Vadas and Steneck 1995). Given the importance of coralline algae as the principal substratum for abalone recruits, any role played by urchins or other grazers in the maintenance of this substratum is of paramount importance. It cannot, however, be assumed that *P. angulosus* fulfils this role, because it seems to be predominantly a drift-feeder that undertakes little active grazing (Day 1998, Day and Branch in prep.).

This survey has emphasized the importance of coralline substrata for the recruits of *H. midae*, and the significance of strongly textured corallines in particular. Taking all types of corallines collectively, recruits do not exhibit as strong a preference for hiding beneath urchins as do juveniles. This does, however, leave open the question of whether urchins, or perhaps other grazers, play an indirect role in maintaining surfaces suitable for settlement (or post-recruit survival), an issue explored by Day (1998) and Day and Branch (in prep.) by way of experimental manipulation of grazers.

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