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EVIDENCE FOR A POSITIVE RELATIONSHIP BETWEEN JUVENILE ABALONE *HALIOTIS MIDAE* AND THE SEA URCHIN *PARECHINUS ANGULOSUS* IN THE SOUTH-WESTERN CAPE, SOUTH AFRICA

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Previous field observations have suggested an association between the urchin *Parechinus angulosus* and juveniles of the abalone *Haliotis midae*. To test the generality and nature of this association, surveys were carried out at five sites between Cape Point and Danger Point in the kelp beds of the South-Western Cape, South Africa. These showed that both species occupy primarily hard substrata, showing preferences for encrusting coralline algae. They also confirmed a strong, positive relationship between urchins and juvenile abalone. Of the juvenile abalone sampled, more than 98% were found beneath sea urchins. All small (3–10 mm) and medium-sized (11–20 mm) juvenile abalone were under urchins, whether on flat or vertical reef, or in crevices. A small proportion (~10%) of larger juveniles (21–35 mm) was not found under urchins, and in these instances they occupied crevices instead. These findings are of particular importance in terms of their implications for the lucrative commercial abalone fishery in South Africa, indicating that urchins are of critical importance to the continued survival of viable abalone populations. There has been a dramatic decrease in natural populations of sea urchins over the past five years in the heart of the abalone fishing grounds, and the present findings suggest that this will lead to recruitment failure of abalone, because juvenile abalone seem dependent on the urchins. The long-term consequences for the industry may be crucial.

As abalone grow, they change their habitat and behaviour (Shepherd and Turner 1985, Prince *et al*. 1988, Tutschulte and Connell 1988). In general, at the end of the larval phase, competent larvae settle preferentially on encrusting coralline substrata (Morse *et al*. 1980, Saito 1981, Shepherd and Turner 1985), and both the specificity of this relationship and the mechanisms involved have been the subject of numerous experiments and debates (Morse *et al*. 1984, Johnson *et al*. 1991, Morse 1991). Once established on encrusting corallines, they feed primarily on benthic diatoms and bacteria (Kawamura *et al*. 1995), and are also imbued with a pink coloration from the coralline algae themselves, rendering them relatively cryptic against the pale corallines (Garland *et al*. 1985, McShane 1992). As they grow, however, their diet changes and their shell markings darken, making them more visible (Tegner and Butler 1989). Lacking both the protective thick shell of larger abalone and the advantages of small size and cryptic coloration (Shepherd and Turner 1985), it is surmised that they must then rely on inaccessibility to predators (Sloan and Breen 1988, Tegner and Butler 1989) and move to habitats offering more concealment (Tegner and Butler 1989, McCormick *et al*. 1994). This transition marks the end of what is defined here as the "recruit" stage and the beginning of the "juvenile" stage, the latter covering individuals of 3–35 mm shell length.

The specific behaviour patterns of juveniles when they outgrow their association with corallines is largely dependent on the type of habitat available to them (Tegner and Levin 1982). This probably accounts for the diversity of biotic associations and habitats of juvenile abalone, which differ among areas, species and communities. Research in several areas has highlighted the fact that the availability of shelter beneath boulders or in crevices is critical for the survival of post-recruits of several abalone species (*Haliotis laevigata* in southern Australia, Shepherd and Turner 1985; *H. iris* in New Zealand, McShane and Naylor 1995; *H. corrugata* and *H. fulgens* in southern California, Tutschulte and Connell 1988; *H. walallensis* in California, Lowry and Pearse 1973; and several haliotid species in New South Wales, Australia, Andrew 1993).

The juveniles of some haliotid species, however, shelter beneath adult sea urchins, rather than under rocks and boulders (Kojima 1981, Tegner and Dayton 1981, Tegner and Levin 1982, Tegner and Butler 1989, Tarr *et al*. 1996). Tegner and Butler (1989) believe that this behaviour is primarily a defence against predators, but drift seaweed caught by sea urchins may also benefit the abalone (Tegner and Dayton 1977). In South Africa, a positive relationship has been reported between juveniles of the commercially exploited abalone *Haliotis midae* and the sea urchin *Parechinus angulosus* (Tarr 1989, Wood 1993, Tarr

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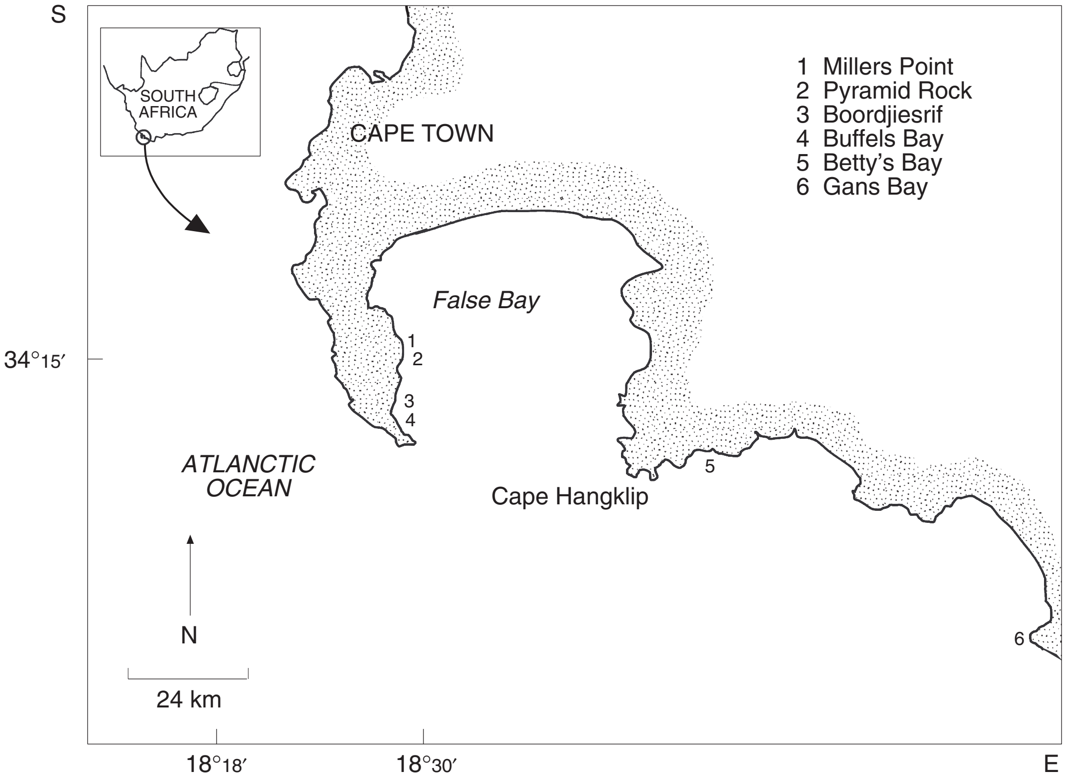

Fig. 1: Map of the South-Western Cape, South Africa, showing the location of the study sites

et al. 1996), with juvenile *H. midae* occurring predominantly under the tests or spine canopies of adult sea urchins on shallow subtidal reefs (Tarr 1995).

Tarr *et al.* (1996) showed that juvenile abalone have virtually disappeared from areas where urchins are depleted. The reason for the decline in urchin numbers is uncertain, but purported increases in populations of rock lobster *Jasus lalandii*, which eat sea urchins, have been mooted as the cause (Tarr *et al.* 1996). It is critical for the management of the fast-dwindling abalone resource that the nature and significance of the association between urchins and juvenile abalone be elucidated.

The primary aim of this paper was to test the generality of the evidence for a close positive relationship between juvenile abalone and sea urchins. As habitat availability influences the behaviour and associations formed by juvenile abalone (Tegner and Levin 1982), the habitat preferences of both species were investigated, in relation to habitat availability. Moreover, because the preferences of abalone for different habitats change with abalone size (McCormick *et al.* 1994), size-based relationships between abalone and habitats were examined, within the specified size range of "juveniles" (i.e. 3–35 mm shell length).

The investigations took the form of surveys, so they provide correlations from which causality at best can only be inferred. Nevertheless, they provided a foundation from which more detailed experimental work, reported on elsewhere (Day 1998, Day and Branch in prep.), could then be based.

MATERIAL AND METHODS

Sites

Five sites were selected between Cape Point and Danger Point for initial surveys of the habitats and ecological associations of abalone juveniles: Millers Point, Boordjiesrif, Buffels Bay, Betty's Bay and Gans

Bay (Fig. 1). A sixth site, at Pyramid Rock, was later sampled (Fig. 1). All sites lay within kelp beds (primarily *Ecklonia maxima*, with some *Laminaria pallida*), and either currently or previously supported populations of sea urchins *P. angulosus* and abalone *H. midae*.

Associations between juvenile abalone, urchins and substratum

An initial set of surveys between May and July 1995 was designed to determine the preferred habitat of juvenile abalone and, specifically, to test the generality of any relationship between juvenile abalone and sea urchins.

A preliminary dive at Betty's Bay failed to detect either urchins or juvenile abalone. At each of the remaining four sites, 38 randomly dropped 50 × 50 cm quadrat samples were read by divers on SCUBA. Quadrats were restricted to reef areas dominated by rock, although where sand patches intruded into the quadrats, they were included in the assessment. Surveys were carried out at depths of 1.0–2.5 m at mean spring low water (MSLW), and were therefore concentrated on the depth range in which the majority of juvenile *H. midae* are found (Newman 1968, Tarr 1989).

For each quadrat, the percentage cover of each substratum type was recorded, along with the numbers of urchins and the numbers and sizes of abalone juveniles found on each particular substratum. Substrata were broadly classified into nine categories, each relating to a texturally or structurally different type of surface. The categories were: (1) sponge, (2) sand, (3) foliar algae, (4) polychaete mat (primarily *Paronuphis antarctica*), (5) bare rock, (6) the encrusting alga *Hildenbrandia lecanellierii*, (7) colonial ascidians, (8) pink encrusting corallines <1 mm thick (grouped as "thin" corallines) and (9) "thick corallines" (thickly layered corallines >1 mm thick and consisting predominantly of *Heydrichia woelkerlingii*). Within each substratum type, the numbers and sizes of abalone exposed, hidden under rocks or in crevices, or under urchins were noted. Percentage cover data were converted into actual areas of each substratum type, and urchin and abalone counts could thus be expressed in terms of densities per unit area of each substratum category.

Data analysis

The number of abalone juveniles found in each quadrat (y) was regressed against the number of urchins in that quadrat (x), using the square-root transformations $y'=\sqrt{(y+0.5)}$ and $x'=\sqrt{(x+0.5)}$, in view of the low numbers involved. A more useful comparison was derived, however, by calculating proportions of abalone found under urchins against the proportion of area occupied by urchins, to test whether juvenile abalone are specifically associated with urchins. χ^2 tests were performed to compare the numbers of abalone found under urchins in each quadrat (observed) with those predicted by the null hypothesis that abalone should occur beneath urchins in proportion to the area occupied by urchins.

The total area occupied by urchins was estimated using the formula:

$$Area = \pi r^2 N \quad ,$$

where r is the mean radius of an urchin (including spine canopy) and N is the total number of urchins found. For a random sample of 60 urchins, r was 35 mm (range 20–45 mm).

The patchy distribution of abalone juveniles meant that a square-root transformation of abalone densities ($x'=\sqrt{(x+0.5)}$) was necessary before two-way ANOVAs could be run on both abalone and urchin data. Tukey *a posteriori* tests were used on any significantly different data.

Use of indices

Gabriel's (1978) index of selectivity (W) was used to determine the relationship between the availability of different substratum types and the proportional abundance of animals on each. This assessed whether urchins or juvenile abalone displayed any selectivity for particular substrata. In logarithmic form, the index (W) yields values that range between $-\infty$ (negative selection) and $+\infty$ (positive selection), with values of 0 indicating an absence of any selection. It is calculated as follows:

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

where $p1$ is the percentage of urchins or juvenile abalone occupying a particular substratum; $p2$ is the percentage of area covered by that particular substratum; $q1 = (100 - p1)$, and $q2 = (100 - p2)$.

Habitat effects on the distribution of juvenile abalone of different sizes

Following the initial surveys, in which "thin" and "thick" encrusting corallines were identified as being preferred by juvenile abalone, more detailed surveys of these substrata were undertaken at Pyramid Rock, Boordjiesrif, Buffels Bay and Millers Point (Fig. 1). This set of surveys examined the possibility that,

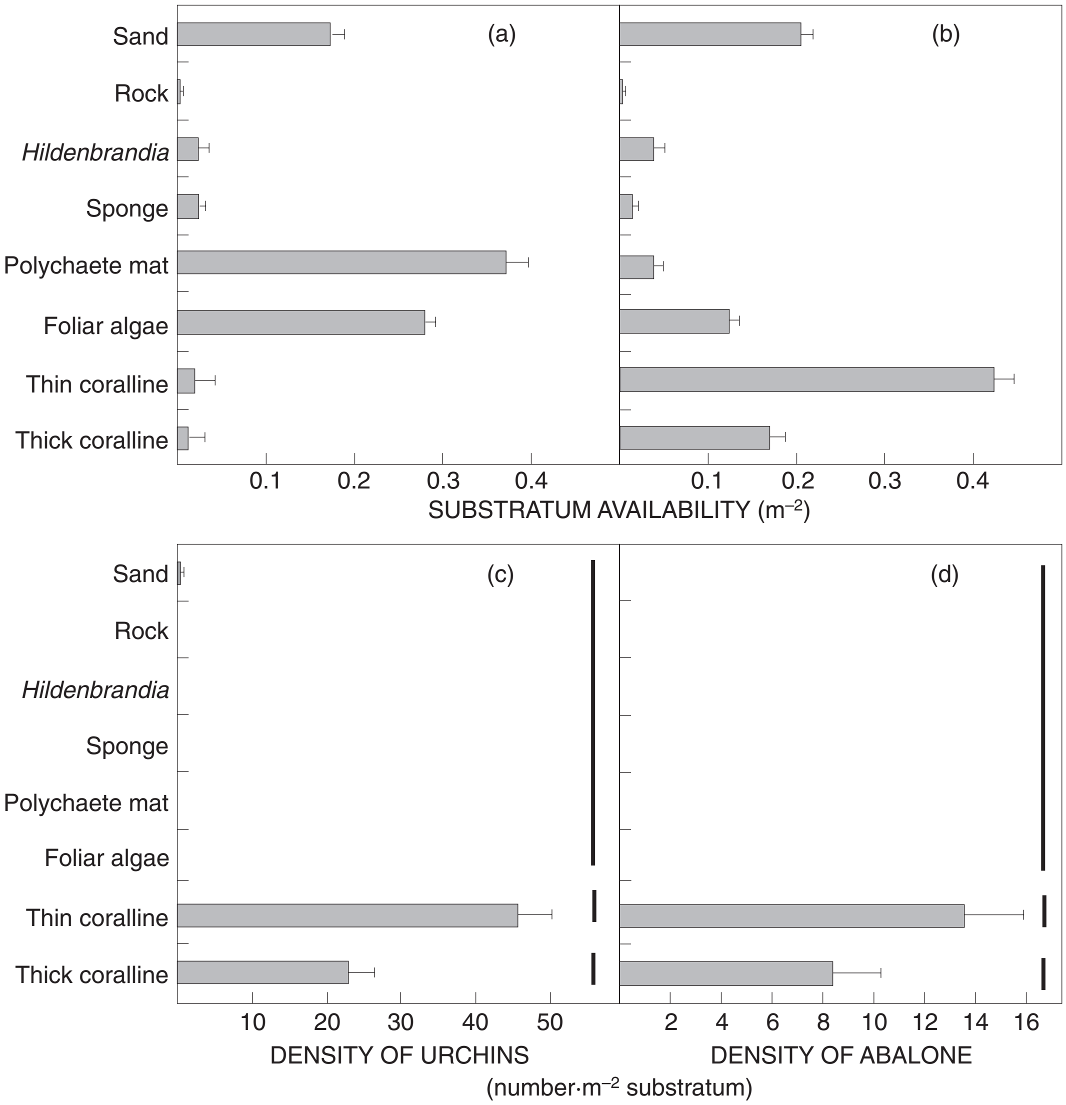

Fig. 2: Results of the broad-scale survey – (a) composition of substratum by area at the Betty's Bay site, (b) composition of substratum by area at sites excluding Betty's Bay, (c) density of urchins on different substrata, excluding Betty's Bay, and (d) density of abalone on different substrata, excluding Betty's Bay. Vertical bars link densities of urchins or abalone on different substrata that were not significantly different (Tukey test, $p > 0.05$). Error bars denote +1*SE*

within the substrata preferred by abalone juveniles, there might be more specific preferences for particular habitat types, related to the degree of shelter provided by each. First, the proportional availability of all habitat types was assessed. At each site, a total of 12 × 8-m transects were swum along a weighted, demarcated rope. The length of each habitat type falling directly under the rope was recorded (to the nearest 5 cm). Habitats included sand, shale, gravel, small rocks (with longest side <10 cm), flat rock, vertical rock, kelp holdfasts, crevices (which included sheltered areas formed between adjoining rocks), "under rock" area, sponge, *Hildenbrandia* patches and polychaete mats. Because shelter was the primary variable being investigated, the categories were subsequently simplified for analysis by retaining the categories flat rock, vertical rock and crevices (including all under-rock surfaces beneath movable boulders), but merging the other categories as "unsuitable habitat", because they did not support juvenile abalone.

At each site, stratified random sampling was applied to habitats, which were classified into three types, according to degree of exposure: crevice habitat (including accessible "under rock" habitat), flat (i.e. horizontal) exposed rock surfaces and vertical exposed rock faces. Any boulder too large to roll was classified as a flat or vertical rock surface. Quadrat size was reduced to 25 × 25 cm to allow more specific coverage of the restricted habitat types. In all, 30 quadrats were read for each habitat category, at each of the four sites. The percentage area constituting each particular habitat was recorded, as well as the size and number of juvenile abalone found in that habitat and whether or not they were under urchins. Numbers of juvenile abalone were recorded in three size categories: small (3–10 mm), medium (11–20 mm) and large (21–35 mm).

Data analysis

The availability of different habitat types at each site was compared, using a two-way fixed-effects ANOVA, on arcsin-transformed data. Because urchins also represented an important habitat type for abalone, their densities in each of the habitats were compared by means of a two-way ANOVA, after square-root transformation. Abalone densities in each habitat were similarly compared.

Data were also expressed in terms of the frequencies of small, medium-sized and large juvenile abalone present in each habitat, and standardized as the number per m^2 of each habitat to allow for differences in the amount of habitat available in any particular quadrat. Two-way ANOVAs were run on the data for each size-class, to test for differences in the distribution of each size-class of juveniles among different habitats.

RESULTS

Associations between abalone juveniles, urchins and substrata

Both abalone juveniles and urchins were absent from Betty's Bay. Most of the reef there, with the exception of small, well-grazed rings around adult abalone, had been colonized by a polychaete tube worm *Paronuphis antarctica*, whose tubes produce a dense mat of shale and sand. Most of the reef at this site was also overgrown by thick stands of foliar algae (Fig. 2a). Consequently, this site was excluded from the analysis of habitat preferences of urchins and juvenile abalone.

Figure 2b–d summarizes the results obtained at the remaining four sites in the initial broad-scale survey. The data have been pooled for clarity, because there were no significant differences between these sites ($p > 0.05$). In terms of substratum availability (Fig. 2b), thin corallines occupied a greater area than did any other substratum. Sand pockets comprised a fairly high proportion of reef area too, although they occurred mainly on the reef periphery. Bare rock occupied a surprisingly small area, with most available reef area being covered by encrusting coralline or foliar algae.

Densities of urchins on different substrata suggested a preference for coralline-covered hard substrata, with all urchins occurring on them, except for a very small number on sand patches (Fig. 2c). Densities of urchins were high, averaging $45.5 \cdot m^{-2}$ on thin corallines and $23 \cdot m^{-2}$ on thick corallines. There were no significant differences between sites ($df = 3$, $p > 0.05$), but there were differences between different substrata ($df = 8$, $p < 0.02$). There were no significant interactions between sites and substrata ($p > 0.05$). Tukey *a posteriori* tests, run on data pooled between sites, showed that densities of urchins on thick and thin corallines differed significantly from those on other substrata and from each other ($p < 0.05$), with highest densities on thin corallines.

Densities of juvenile abalone on different substrata followed a similar pattern to those of urchins, with the highest densities being found on thin corallines, followed by thick corallines. Juvenile abalone were not found on any of the other substrata (Fig. 2d). Distributions were, however, extremely patchy. A two-way ANOVA showed no significant differences in abalone densities between sites ($df = 3$, $p > 0.05$), although differences among substrata did differ significantly ($df = 8$, $p < 0.01$). There were no significant interactions between sites and substrata ($p > 0.05$). Abalone densities on both thick and thin corallines were significantly different ($p < 0.05$) from each other, and from all other substrata.

Substratum selectivity

Figure 3 shows the proportions of urchins and abalone juveniles found on different substrata, plotted against the relative availability of each substratum, as well as the selectivity indices for the two species. Negative selectivity was shown by both urchins and abalone for most substrata, with the exception of thick and thin corallines, for which there was strong, positive selection. Whereas thin corallines occupied

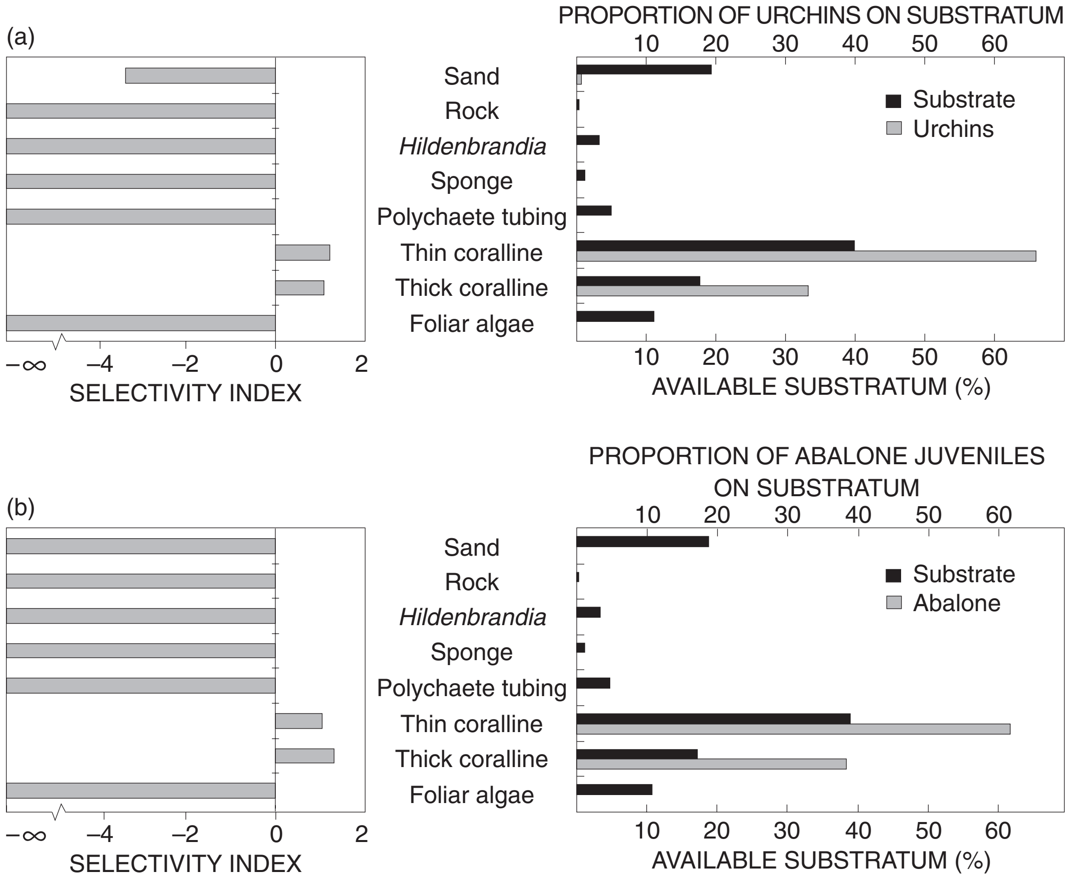

Fig. 3: Substratum selection by (a) urchins and (b) juvenile abalone. The left-hand graphs show the selectivity indices of urchins and juvenile abalone for each substratum. The right-hand graphs show the proportional distribution of urchins and juvenile abalone on different substrata, compared to the proportional availability of each substratum. Negative selectivity values indicate rejection or avoidance and positive ones show preferences for a particular substratum

approximately 36% of the total available reef surface, 66% of urchins and 61% of juvenile abalone occupied this substratum. Similarly, only 14% of the reef was occupied by thick corallines, but 33% of urchins and 38% of abalone were found on them.

Associations between juvenile abalone and urchins

Most juvenile abalone were found under urchins. Figure 4 illustrates the significant relationship between urchin and juvenile abalone densities at different sites ($r^2 = 0.2878$ for transformed data, $n = 152$, $p < 0.05$).

Table I compares the proportion of abalone found under urchins with the percentage of substratum occupied by urchins. A strong, positive relationship exists between urchins and juvenile abalone, virtually all juvenile abalone being found under urchins, even though urchins occupied only 18–25% of the substratum area. This finding was consistent and significant at all sites (χ^2 test: $p < 0.001$).

Distribution of abalone and urchins in different habitats

There were no differences in urchin densities between sites ($df = 3$, $p > 0.05$) and no significant interactions between sites and substrata ($p > 0.05$). However, urchin densities differed significantly between

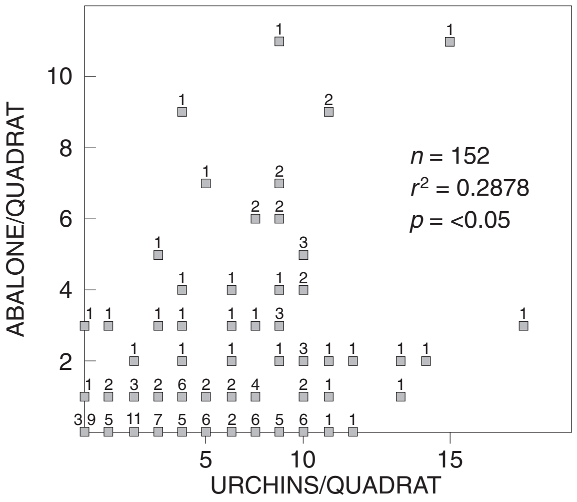

Fig. 4: Relationships between juvenile abalone and urchin densities. The number above each point indicates the number of samples with this value

habitats ($df = 2$, $p < 0.05$), being highest in crevices ($112.4 \pm 46.4 \cdot m^{-2}$; Tukey test, $p < 0.05$), but similar on flat and vertical rock faces ($75.88 \pm 24.57 \cdot m^{-2}$ and $75.7 \pm 26.40 \cdot m^{-2}$ respectively, Tukey test, $p > 0.05$). Similarly, densities of abalone juveniles (of all sizes) differed significantly between habitats ($df = 2$, $p < 0.01$), higher densities being found in crevices than on flat or vertical rock faces ($p < 0.05$). Densities of juvenile abalone at Pyramid Rock and Buffels Bay were significantly different from each other.

Figure 5a shows the relative availability of crevices, flat and vertical rock faces, pooling data across sites because there were no significant differences between them ($df = 3$, $p > 0.05$). Availability of these three habitat types, however, differ significantly ($df = 2$, $p < 0.05$), flat rock being the most abundant habitat (Tukey test, $p < 0.05$), and crevice and vertical rock habitat being equally abundant ($p > 0.05$). If the availability of sheltered habitat (i.e. crevices) is compared to the total exposed habitat (vertical and flat rocks), there was, however, significantly less sheltered than exposed habitat ($df = 1$, $p < 0.005$). The crevice area, which is the only one offering physical cover to urchins and abalone, was in fact a fairly small component of the whole reef environment, constituting <25%.

Effect of abalone size on habitat choice

When juvenile abalone were considered in terms of three size groups, there were also differences in the types of habitat that they occupied. Figure 5b shows the frequencies of small, medium-sized and large juvenile abalone in the three habitat-types, separating those that were under urchins from those that were not. Small and medium-sized juveniles all occurred under urchins. A small proportion of large juveniles was not found under urchins, all occupying crevices. All juveniles were thus cryptic, only being found on exposed flat or vertical surfaces if they were concealed under urchins. In general, more large juveniles were found in the crevice habitat than in any other habitat.

Two-way ANOVAs were run separately on the distributions of each of the three size-classes of juvenile abalone in flat, vertical and crevice habitats. Although some differences in densities between sites were evident, overall, only large animals were found in significantly higher densities in crevices, as opposed to vertical or flat rock faces ($df = 2$, $p < 0.001$), whereas there were no significant differences in the distribution of small and medium-sized abalone between the three habitats.

DISCUSSION

Associations between juvenile abalone, urchins and substrata

The importance of encrusting corallines as a substratum for both the urchin *P. angulosus* and juvenile

Table I: Results of χ^2 tests run on the number of abalone juveniles found under urchins versus the expected number, based on the proportion of the area of each quadrat occupied by urchins

Site	Number of quadrats	Percentage cover of substratum by urchins (±*SE*)	Percentage of juvenile abalone under urchins		*p*
			Predicted	Actual (±*SE*)	
Boordjiesrif	15	23.47 (3.86)	23.47	100.00 (0)	< 0.001
Buffels Bay	24	20.95 (2.02)	20.95	99.17 (0.83)	< 0.001
Millers Point	20	22.47 (2.55)	22.47	100.00 (0)	< 0.002
Gans Bay	7	23.79 (2.98)	23.79	100.00 (0)	< 0.001

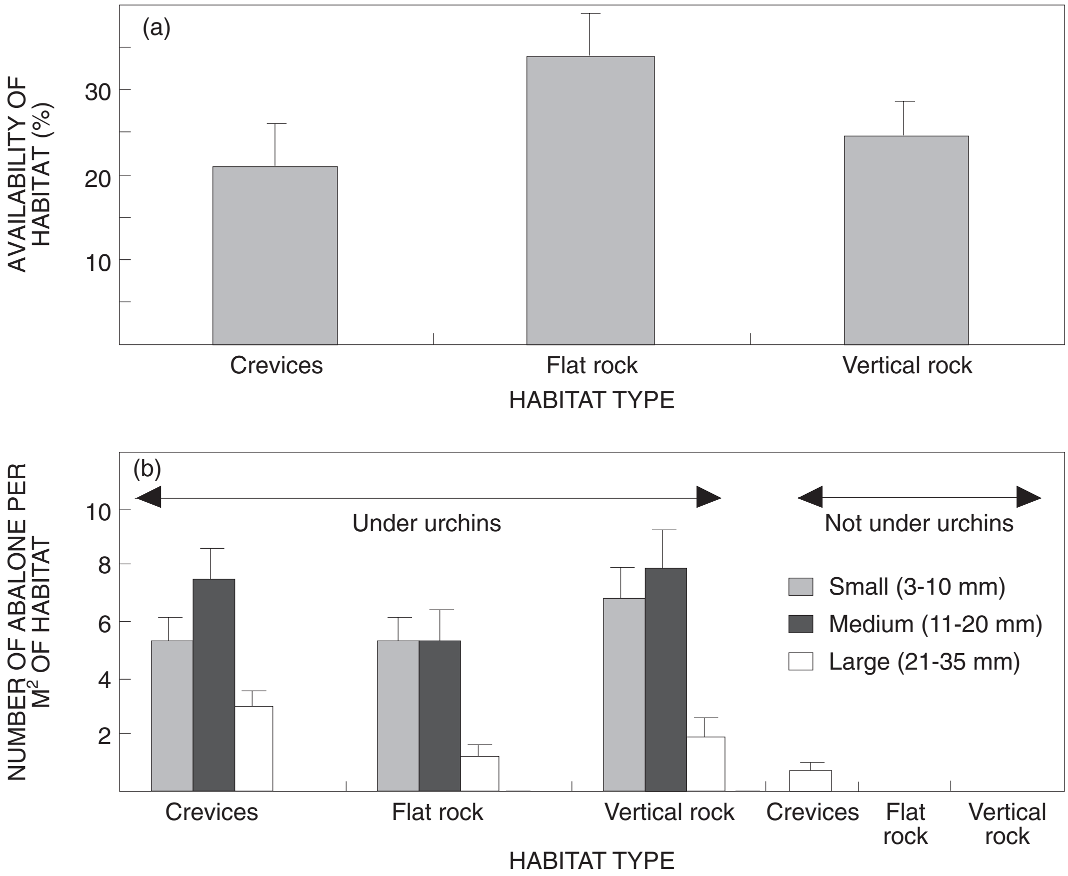

Fig. 5: Variations in size frequencies of juvenile abalone with different habitats – (a) proportional availability of hard-reef habitats occupied by juvenile abalone, out of total reef habitat ("unsuitable habitat" not shown here), and (b) numbers of abalone in each size-class in each habitat type. The numbers of abalone from each size-class that were not found under urchins in each habitat are shown. Error bars denote +1*SE*

H. midae is clearly evident from the results (Figs 2, 3). In many parts of the world, urchins have been attributed the role of maintaining coralline cover, often linked to their ability to overgraze kelp forests or foliar algae (reviewed by Lawrence 1975, Harrold and Pearse 1987). This role has, however, been debated (Contreras and Castilla 1987), particularly where urchins are reputed to trap drift seaweeds rather than actively graze on the substratum. Nevertheless, urchins frequently do play a role in defining their habitat structure (Fletcher 1987, Andrew and Underwood 1992, Hagen 1995). In the present case, whereas the occurrence of urchins on encrusting corallines might reflect habitat preference, it could also be explained by habitat creation, if the urchins themselves are responsible for maintaining these corallines. Because the present surveys yield only correlative data, they cannot distinguish between the two possibilities.

The absence of both abalone juveniles and urchins from virtually all non-coralline substrata sampled was not surprising, owing to the unsuitability of such substrata for grazing and occupation. Shepherd (1973) observed extremely low densities of urchins on alcyonaria-covered reef, and none at all on sponges, whereas Fricke (1979) found that hard substrata were of prime importance in explaining densities of *P. angulosus* in False Bay. However, it is noteworthy that the densities reported by Fricke (1979) are considerably higher (up to $72 \cdot m^{-2}$) than those found in the present survey.

Tegner and Butler (1989) noted that juvenile abalone do not attach well to silty surfaces and are therefore found only on clean rock surfaces. Shepherd and Turner (1985) also observed no juvenile abalone on upright corallines or foliar algae, possibly because smooth, hard surfaces are necessary for secure pedal adhesion and attachment (Shepherd and Daume 1996).

There are two plausible reasons for the habitat "choice" exhibited by juvenile abalone. The first implies selection by juveniles for the coralline substratum itself, as circumstantially suggested by the positive selectivity indices in Figure 3b. Alternatively, the occurrence of juveniles on corallines may be incidental, and juveniles may actually be selecting urchins that happen to inhabit that substratum. There was a significant correlation between urchin and abalone densities (Fig. 4). This correlation does not, however, answer the question of whether juvenile abalone and urchins merely select the same kind of habitat, or whether one is actively seeking out the other. By contrast, Table I shows that, not only are abalone juveniles correlated with densities of urchins, but almost all of them (98–100% at all four sites) are found under urchins, even though urchins covered only 18–25% of the substratum. Conversely, although most of the habitat not covered by urchins still consisted of encrusting corallines, extremely few juveniles were found there.

Further circumstantial evidence to reinforce the suggestion that a close association exists between abalone juveniles and urchins was the lack of both at Betty's Bay. Their joint absence corroborated the results of surveys in the area by Marine & Coastal Management (MCM, formerly Sea Fisheries Research Institute), which previously regularly recorded large populations there (Newman 1968), but which have declined considerably in recent years (Tarr *et al.* 1996). The abundance of foliar algae and extensive polychaete mats (Fig. 2a) at Betty's Bay during the present survey contrasts with the sparsity of both at all other sites (Fig. 2b), and also with previous surveys at Betty's Bay. Field *et al.* (1980) recorded virtually no foliar algae or polychaete mats there in 1976. The marked decline of both urchins and juvenile abalone at Betty's Bay may therefore be associated with this dramatic change in habitat structure and suggests that, in the complete absence of urchins, abalone juveniles either fail to recruit or, if they recruit, failed to survive to juvenile sizes.

The apparent selectivity displayed by juvenile abalone for encrusting corallines at the remaining four sites may therefore be a surrogate for their selection of urchins, which happen themselves to live on encrusting corallines. Consequently, the relationship between *H. midae* juveniles and *P. angulosus* suggested by Tarr *et al.* (1996) appears to be a direct and causal one, and of considerable ecological importance. Of more practical relevance, these findings validate the protocols followed during previous MCM surveys of abalone juveniles, in which the only habitat searched to obtain estimates of the densities of juvenile abalone was that under urchins.

Size-related associations between abalone juveniles, urchins and habitat

Two possible causes of the correlative relationship between abalone juveniles and sea urchins emerge from a consideration of different sized abalone. All small and medium-sized abalone juveniles were beneath urchins. Although not all large abalone juveniles were found under urchins, those that were not were concealed in cracks and crevices. The association between abalone juveniles and urchins therefore appears to be predominantly shelter-related, a view shared by Breen *et al.* (1985) and Tegner and Butler (1989).

The importance of shelter for the survival of juvenile abalone cannot be overestimated. Caddy and Stamatopoulos (1990) suggest that the carrying capacity of different habitats is largely dependent on the availability of shelter for individuals of different sizes. Kojima (1981) noted that juvenile survival varied directly with the degree of shelter provided by the environment. In the present case, it appears to be urchins that are fulfilling this role, rather than physical shelters. The most compelling indication for this comes from the fact that the juveniles most vulnerable to predation (i.e. small and medium-size) invariably occurred under urchins (Fig. 5a). Juveniles of other abalone species that do not conceal themselves under urchins all shelter under boulders (Lowry and Pearse 1973, Dayton 1975). At the sites surveyed in this study, there was a paucity of this under-boulder habitat, largely because dense mats of sand and shale cemented rocks to the substratum. These mats were created by tubiferous polychaete worms, primarily *P. antarctica*. The sparsity of "under-rock" habitat reinforces the potential importance of the urchins as a shelter, particularly for small abalone.

For large juvenile abalone, crevices provide some protection, whether or not urchins are present. It is after this "large-juvenile" stage that sub-adult abalone (>35 mm shell length) begin to lose the photophobia of juvenile abalone and emerge from cryptic habitats to inhabit areas of exposed reef. By that stage, their shells are sufficiently robust to offer protection against at least some predators (Tegner and Butler 1989).

Implications of the association between juvenile abalone and urchins

Thus far, the association observed between abalone juveniles and sea urchins has been attributed largely to the degree of protection from predation offered by the urchins. Witman (1985) affirms that the ability of "structures" to provide refuges from predation can explain local distribution and abundance patterns. Tegner and Dayton (1977) found that juvenile urchins protected by adult spine canopies survived far longer than unprotected juveniles. Tegner and Butler (1989) and Breen *et al*. (1985) believe that the occurrence of juvenile abalone and juvenile urchins under adults of the urchin *Strongylocentrotus franciscanus* is primarily to avoid predation.

There are, however, several additional advantages that such a relationship might hold for juvenile abalone. One possibility is that abalone might benefit from drift kelp caught by urchins (Tegner and Butler 1989). Clearly, in the present context, this would depend on whether *P. angulosus* feeds predominantly by grazing, or by trapping kelp. Wood and Buxton (1996), working on *H. midae* in the Eastern Cape, South Africa, suggested that *P. angulosus* is a nocturnal grazer. However, their region of study lies beyond the geographic range of subtidal kelp beds, and urchins might therefore be expected to favour a different mode of feeding there. Although Fricke (1979) described *P. angulosus* in False Bay as a "grazer", he expanded this definition to note that it does feed on pieces of drift kelp, a phenomenon also observed in the present study. The extent to which *P. angulosus* makes use of drift seaweeds is therefore of importance in determining its potential impacts on algae, as well as its possible contribution to the diet of juvenile abalone. As abalone grow, they move onto a diet of macro-algae (Wood and Buxton 1996), and it is at this point that additional food trapped by urchins might be of value, particularly if juvenile abalone would otherwise be too small to be able to trap it themselves. Tegner and Levin (1982) noted increased growth rates of abalone associated with urchins.

There are also other potential advantages that might accrue to abalone from their association with urchins. At the sites surveyed here, sea urchins were found in shallow subtidal aggregations on coralline-encrusted reefs, mainly within beds of the kelp *Ecklonia maxima*. These kelp beds may have considerable implications for the distribution of sea urchins and, hence, abalone juveniles. For example, kelp beds have an important breakwater effect on subtidal communities (Velimirov *et al*. 1977). Urchin populations that occur in exposed areas lacking kelp beds are frequently controlled by the availability of crevices in which they can shelter from the surge (Shepherd 1973, see Farquhar 1994 for *P. angulosus* in the Eastern Cape). However, in the areas surveyed here, urchins were usually encountered on exposed rock surfaces, both flat and vertical, with only a minority clustering in crevices. Only in conditions of extreme swell did divers observe urchins aggregating in crevices, presumably for shelter. Therefore, the normally sheltered conditions in kelp beds may enable urchins to spread out away from crevices. Incidentally, this may also disperse the abalone that take refuge under these urchins. If the benthic material grazed by abalone is in limited supply, such dispersal will ensure that grazing is not restricted to crevices and their immediate vicinity. In addition, if abalone juveniles are able to derive food from kelp trapped by urchins, they may be able to shorten or even do away with periods when they would otherwise have to leave the protection of an urchin to forage (Shepherd and Daume 1996).

In summary, this paper has shown:

(i) that both urchins and juvenile abalone are found predominantly on encrusting corallines;
(ii) a strong, positive relationship between urchins and abalone juveniles, which seems to be attributable to a positive selection of urchins by juvenile abalone;
(iii) that both urchins and juveniles are found in higher densities in crevices than on exposed surfaces;
(iv) that large juvenile abalone are predominantly crevice-dwellers, where they may or may not shelter directly under urchins; and
(v) that small and medium-sized abalone juveniles in kelp-dominated ecosystems are almost always found under urchins and show no preferences for physical shelters, such as crevices and cracks.

The practical import of the findings is considerable. The association between juvenile abalone and urchins is so strong in the region investigated that, were urchins to be eliminated or substantially reduced, a complete collapse of juvenile abalone can be forecast. Indeed, the surveys of Tarr *et al*. (1996) have shown just this at many sites east of Cape Hangklip (Fig. 1), where increases in the density of the West-Coast rock lobster *J. lalandii* have been held responsible. Whatever the cause, these declines have taken place in the heart of the commercial abalone fishing grounds and constitute a serious threat to future recruitment to the fishable stocks.

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