WILEY

Effects of Sea Urchins (Parechinus angulosus) on Recruits and Juveniles of Abalone
(Haliotis midae)
Author(s): E. Day and G. M. Branch
Source: *Ecological Monographs*, Vol. 72, No. 1 (Feb., 2002), pp. 133-149
Published by: Wiley
Stable URL: http://www.jstor.org/stable/3100089
Accessed: 27-06-2016 14:26 UTC

REFERENCES
Linked references are available on JSTOR for this article:
http://www.jstor.org/stable/3100089?seq=1&cid=pdf-reference#references_tab_contents
You may need to log in to JSTOR to access the linked references.

EFFECTS OF SEA URCHINS (*PARECHINUS ANGULOSUS*) ON RECRUITS AND JUVENILES OF ABALONE (*HALIOTIS MIDAE*)

E. Day and G. M. Branch[1]

Marine Biology Research Institute, Zoology Department, University of Cape Town, Rondebosch 7701, South Africa

Abstract. Much current research on community ecology concerns indirect effects, cascading trophic interactions, and the role of top-down vs. bottom-up processes, as well as subsidization of matter and energy between different systems. We addressed all these topics by exploring interactions between the urchin *Parechinus angulosus* and both recruits and juveniles of the abalone *Haliotis midae,* in the light of the fact that juvenile abalone shelter beneath the urchins. In field experiments at six sites, urchins were eliminated from removal plots to determine the degree to which juvenile abalone (individuals 3–35 mm in length) depend upon urchins. Comparisons were made with undisturbed and disturbance-control plots. We hypothesized that after removal of urchins: (1) there would be an immediate decline of juvenile abalone, since they are intimately associated with the urchins; (2) abalone recruits (recent settlers <3 mm in length) would be unlikely to suffer immediately or directly because, unlike juveniles, they are only weakly associated with the urchins; (3) foliar algae would proliferate due to decreased grazing by urchins; (4) there would be a consequent reduction in crustose coralline algae due to overgrowth by foliar algae; and (5) the decline of crustose corallines would reduce recruitment of abalone due to a loss of settlement and nursery habitat. In urchin-removal plots, juvenile abalone declined dramatically, becoming virtually extinct locally. Their disappearance was slowest in crevices compared with exposed habitats, but even there they failed to survive longer than five months. Contrary to expectations, abalone recruits also disappeared from urchin-removal plots, possibly because the cover of sediment almost doubled there. Also contrary to our hypotheses, neither foliar macroalgae nor encrusting corallines responded to urchin removal. The explanation of these results is that *P. angulosus* was able to gather drift kelp when this food source was available, rather than acting as an active grazer. This feeding pattern has profound consequences and explains why urchins failed to influence algal community composition. By sheltering beneath urchins, juvenile abalone gain protection from predators and may also benefit from an enhanced food supply. Bottom-up subsidization of urchins by drift kelp is thus responsible for the feeding behavior of the urchins, and indirectly facilitates their role in harboring juvenile abalone. This role is of immense importance for the lucrative abalone fishery, and depletion of urchins could lead to a collapse of abalone populations. Human exploitation of top predators that consume urchins, such as rock lobsters and some fishes, has conceivably exaggerated the role of urchins in sustaining juvenile abalone.

Key words: abalone; bottom-up effects; commensalism; Haliotis midae; *indirect effects; kelp;* Parechinus angulosus; *subsidization; trophic interactions; urchins.*

INTRODUCTION

Three issues are currently central to much research on community structure and dynamics. The first concerns the frequency and importance of indirect effects, in which the direct impact of one species on another may have indirect positive or negative effects on a third species (Holt 1977, Wootton 1994, Menge 1995, 1997). Indirect effects can be broadly divided into density-mediated effects that yield changes in abundance and trait-mediated effects that result in alterations of behavior or physiology (Abrams et al. 1996).

The second issue focuses on the nature of cascading interactions among the trophic levels of food webs.

This focus was sparked by Hairston et al. (1960), who suggested that much of the world is dominated by plants because predators control herbivores that would otherwise check plant growth: the "green world" hypothesis (Pimm 1991). Implicit in this view is the assumption that top consumers play a dominant role in controlling community structure, hence the term "top-down" control. This hypothesis is not without controversy (e.g., Hairston and Hairston 1993, Persson et al. 1996, Polis and Strong 1996). It has, however, spawned a third issue, namely the relative importance of top-down vs. bottom-up control, the latter concerning the degree to which nutrient supplies and productivity influence community structure and function. Although initially cast in opposition, these two views are not mutually exclusive. Indeed, interactions between top-down and bottom-up processes are increasingly being reported (Persson et al. 1996, Menge et al. 1999, Menge

133

2000). Of particular relevance are recent modifications of these models, which incorporate the influences of "subsidies" of material and energy flowing between or within ecosystems (Bustamante et al. 1995, Bustamante and Branch 1996, Polis and Strong 1996), as well as the effects of positive interactions such as mutualism and commensalism (e.g., Dethier and Duggins 1984, Bertness and Callaway 1994).

This paper addresses all three issues, with a central focus on interactions within kelp beds, particularly between the urchin *Parechinus angulosus* and both juveniles and recruits of the South African abalone *Haliotis midae*. The ability of sea urchins to influence community structure has been well documented in many parts of the world, including the effects of natural increases or declines in urchin populations (Bernstein et al. 1981, Tegner and Levin 1983, Witman 1985, Contreras and Castilla 1987, Hagen 1995, Vadas and Steneck 1995), and field experiments manipulating urchin densities (Breen and Mann 1976, Tegner and Dayton 1977, Ayling 1981, Dayton 1985a, Andrew and Underwood 1992, Camus 1994, Hagen 1995). Most of these reports indicate a close relationship between urchin grazing and the maintenance or creation of large defoliated areas covered only by encrusting corallines, often referred to as "barrens." Numerous studies have noted dramatic increases in subtidal macroalgae, coupled with a decrease in encrusting corallines, in areas from which urchins were excluded (Jones and Kain 1967, Fletcher 1987, Johnson and Mann 1988, Morrison 1988, Benedetti-Cecchi et al. 1998). Fricke (1979) conducted preliminary urchin-exclusion experiments at Millers Point in False Bay, close to our research sites on the eastern side of the Cape Peninsula of South Africa, and observed an increase in the number of sporlings of the kelp *Ecklonia maxima*. He noted that the turbulent sea conditions in this area prevented urchins from grazing on live kelp fronds, and that the main influence of urchins was on early stages of kelp sporophytes.

The role of urchins in creating barren grounds is, however, not universal, and Branch and Moreno (1994) highlight the risks of generalizing about such causal relationships. For instance, experimental removal of both *Echinometra matthaei* in western Australia (Prince 1995) and *Loxechinus albus* in Chile (Castilla and Moreno 1982) had little effect on macroalgae. In fact, various authors have suggested that many species of urchins only trap drift algae and are never grazers (Velimirov et al. 1977, Velimirov and Griffiths 1979, Dayton 1985a). These observations led Steinberg (1995) to describe urchins as "all-or-nothing herbivores," having either profound impacts on their habitat when they act as active grazers, or none at all, when they passively rely on drift macroalgae.

Other species of urchins can change from drift trappers to active grazers. This switch can be triggered by increases in the density of urchins, which then graze macroalgae unsustainably. Alternatively, disturbance-induced loss of kelp beds can result in a shortage of drift kelp, and change the behavior of urchins from sessile drift feeding to active unsustainable grazing on the remaining plants (Lawrence 1975, Lawrence and Sammarco 1982, Ebeling et al. 1985, Harrold and Reed 1985, Harrold and Pearse 1987, Johnson and Mann 1988, Vadas and Elner 1992). Changes in either the density or behavior of urchins may be caused by alterations in predation pressure, as documented for lobsters (Vadas and Steneck 1995), sea otters (Estes and Palmisano 1974) and, indirectly, killer whales (Estes et al. 1998).

The effects of urchins on benthic species composition and relative abundance are thus variable. Nevertheless, their potential maintenance of encrusting corallines by actively grazing on foliar algae is of particular relevance because coralline algae have been implicated as important settlement sites for various invertebrate larvae, including those of abalone (Shepherd 1973, Saito 1981, Tarr et al. 1996).

The cascade of direct and indirect effects that urchins may have on communities of subtidal kelp beds is of special interest (Harrold and Reed 1985, Sala et al. 1998). In South Africa, field correlations (Day and Branch 2000a) and observational evidence (Tarr et al. 1996) both point to a strong relationship between the urchin *P. angulosus* and juveniles of *H. midae* (defined here as individuals of 3–35 mm shell length). Links also exist between encrusting coralline algae and *H. midae* recruits (i.e., recent settlers <3 mm shell length; Day and Branch 2000b). Of particular concern recently has been a drastic decline in urchin numbers at some monitored sites, closely mirrored by a fall in numbers of juvenile abalone (Tarr et al. 1996). It is possible, therefore, that an absence of urchins could lead to a collapse of *H. midae* populations.

Two potential benefits might accrue to abalone juveniles via their relationship with urchins, namely, protection from predation and access to additional food captured by sea urchins (Tegner and Dayton 1977, Breen et al. 1985, Tegner 1989). Tegner and Levin (1982) suggested that any nutritional benefits will be dependent on the availability of food supplies to the urchins themselves. When drift kelp is limiting, urchins reputedly scour the substratum for microflora, which may have negative effects on small grazers such as juvenile abalone, either because of competition for food, or because of bulldozing effects by the grazing urchins.

The nature of interactions between urchins and abalone juveniles and recruits is thus complex and, in some cases, indirect. The impact of any decline in urchin numbers on abalone will clearly depend on (1) the extent to which juvenile abalone actually derive protection or enhanced food supplies from the association, and (2) the degree to which urchins are responsible for
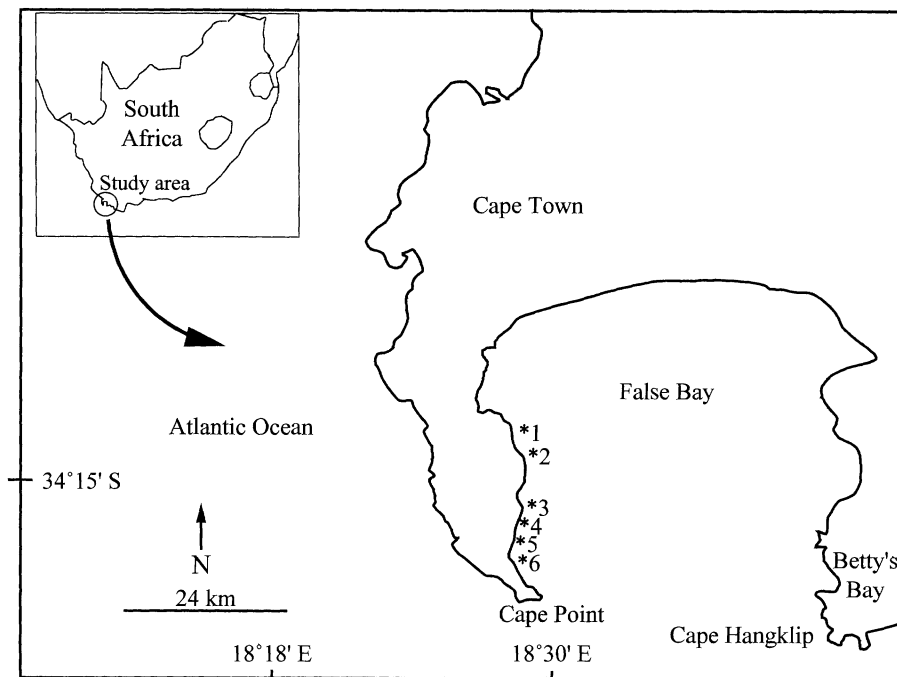
FIG. 1.   Map showing locations of study sites, indicated by numbers: 1, Millers Point (Millers); 2, Pyramid Rock (Pyramid); 3, Boordjiesrif-A (Boordjies-A); 4, Boordjiesrif-B (Boordjies-B); 5, Buffels Bay-A (Buffels-A); 6, Buffels Bay-B (Buffels-B).

maintaining the encrusting corallines upon which abalone settlers and recruits depend.

In this study, we used urchin-removal experiments to explore the mechanisms behind the apparent relationship between juvenile *H. midae* and the urchin *P. angulosus*. Specifically, we tested the following series of hypotheses. (1) Abalone juveniles depend on urchins for shelter from predators, and removal of urchins will have immediate and direct negative impacts on their survival. (2) Abalone recruits are less likely to be directly affected by a decline in urchin numbers than abalone juveniles, because they have a much weaker association with urchins (Day and Branch 2000*b*). (3) Urchins will control macroalgal standing stocks, and the removal of urchins should result in an increase in foliar algae. (4) Removal of urchins will lead to an overgrowth of encrusting coralline algae by proliferating foliar algae. (5) As a consequence, abalone recruits will suffer indirectly as they depend on these corallines for settlement and feeding, and recruitment will decline in the long term.

Although focusing on urchins and abalone, our results have broad implications in terms of addressing the three issues outlined at the outset: indirect effects, cascading interactions among trophic levels, and top-down vs. bottom-up controls. The extent to which multiple ecological interactions yield predictable outcomes is a subject of intense current interest (Wootton 1994). In this instance, complex and often indirect effects made it impossible to predict many of the consequences

of urchin removal; only through manipulative field experiments was their importance elucidated. Furthermore, *H. midae* forms the basis of a lucrative commercial fishery (Tarr 1989), so that any interspecific interactions that affect this species are of profound commercial significance. Finally, the results draw attention to the fact that whole ecosystem effects must be considered in fisheries management; single-species approaches are not adequate on their own (Larkin 1996).

METHODS

Study sites

Six replicate sites were selected on the eastern side of the Cape Peninsula of South Africa (Fig. 1): Millers Point (Millers), Pyramid Rock (Pyramid), Boordjiesrif-A (Boordjies-A), Boordjiesrif-B (Boordjies-B), Buffelsbaai-A (Buffels-A) and Buffelsbaai-B (Buffels-B). The sites were chosen randomly, but all lay within kelp beds, had a wide expanse of subtidal rocky reef, and sustained populations of both urchins and juvenile abalone. Two species of kelp occurred in these kelp beds, *Ecklonia maxima* and *Laminaria pallida,* but the former dominated in the shallow areas where juvenile abalone were most common (Velimirov et al. 1977). During the study, adult kelps were the dominant algae at all of the study sites, with a density of 1–3 adult plants/m². The rocky substratum was covered mainly by encrusting corallines (52% cover), with encrusting red algae, foliar

TABLE 1. Sampling design and frequency for different variables in experimental treatments.

Variable	Sampling unit	Samples per plot	Measure	Initial	3 wk	2 mo	4 mo	5 mo	2 yr
Target species									
Urchins									
On all substrates	whole plot	1	no./m²	+					
On suitable substrates	0.25 × 0.25 m	10	no./m²	+	+	+	+	+	+
Abalone juveniles									
On suitable substrates	0.25 × 0.25 m	10	no./m²	+	+			+	+
On particular habitats	0.25 × 0.25 m	30	no./m²	+	+			+	+
Abalone recruits									
On suitable substrates	0.25 × 0.25 m	20	no./m²				+		
Substrate cover									
Kelp sporelings	0.5 × 0.5 m	8–10	no./m²	+	+	+		+	+
Sand	0.5 × 0.5 m	8–10	% cover	+	+	+		+	+
Polychaete tubing	0.5 × 0.5 m	8–10	% cover	+	+	+		+	+
Crustose corallines	0.5 × 0.5 m	8–10	% cover	+	+	+		+	+
Foliar algae	0.5 × 0.5 m	8–10	% cover	+	+	+		+	+
Kelp holdfasts	0.5 × 0.5 m	8–10	% cover	+	+	+		+	+
Sponge	0.5 × 0.5 m	8–10	% cover	+	+	+		+	+
Sediment	0.5 × 0.5 m	8–10	% cover					+	+
Drift kelp	whole plot	1	mass/plot					+	+
Shelter	4-m transect	4	% length	+					

Note: Plus (+) symbols indicate that the variable was sampled at indicated times.

algae, sponges, compound ascidians, or a thin covering of sediment comprising the balance (Day and Branch 2000b). Several of these sites had previously been surveyed for correlations between juvenile abalone and urchin abundance (Day and Branch 2000a). Both the urchins and juvenile abalone occurred exclusively on encrusting corallines, and 97% of the juvenile abalone were concealed beneath urchins, even though the latter occupied only 25% of the substratum. No juvenile abalone <20 mm in length were found in any other forms of shelter (i.e., in crevices or beneath boulders), and even in the case of larger juveniles (21–35 mm), >90% were found beneath urchins (Day and Branch 2000a). Surveys at Millers Point revealed that abalone recruits exhibited a weaker, but still significant, relationship with urchins: 25–80% of recruits occurred beneath urchins, the proportion being highest when the urchins occupied smooth rather than textured encrusting corallines (Day and Branch 2000b)

Experimental design

Three treatments were established at each site in August 1995, one treatment per plot, with a total of three plots per site. Each plot comprised a 4 m radius circle, positioned at a depth of ~1.5 m below mean low-water spring tides. The plots were set parallel to the shore, ≥10 m apart, and thus spatially independent. The three treatments consisted of (1) undisturbed controls, (2) disturbance controls and (3) urchin removals. In the urchin-removal treatment, SCUBA divers removed all urchins from within the plot, and transported them ≥15 m away from any of the plots. In the disturbance control, urchins were removed from the substratum, but then left lying close to their original positions, where they reattached themselves. This allowed assessment of any short-term impact of disturbance associated with

diver activities during urchin removal. The undisturbed controls were not manipulated. The size of the plots was sufficient to counter re-invasion of urchins to the urchin-removal plots, ensured independence of samples taken within each plot, and guarded against repeat-sampling affecting the survival of juvenile abalone. Any urchins that entered the urchin-removal plots were removed during subsequent sampling periods. Urchin movement into cleared areas was, however, very slow. Fewer than 10 urchins had to be removed from all six urchin-removal plots on each sampling occasion, even after two years had elapsed.

Sampling methods

Four sampling procedures were used, and their design and timing are summarized in Table 1.

Urchins and juvenile abalone.—Three different strategies were used to sample urchins and juvenile abalone. Firstly, before treatments were initiated, a total count was made of all urchins in each plot. Secondly, ten 0.25 × 0.25-m quadrats were randomly placed in each of the three plots at each site, and sampled for both urchins and juvenile abalone. The positions of juvenile abalone (beneath urchins, exposed, or concealed elsewhere) were recorded. Since this procedure involved lifting urchins to search for the abalone, there was the potential to disturb both the urchins and the abalone. The risk of this effect influencing later results was minimized by undertaking the sampling a limited number of times: initially, after 3 wk, after 5 mo, and after 2 yr (Table 1), and by sampling only 5% of the plot. The absence of any differences between undisturbed control and disturbance-control plots (see *Results*) is strong evidence that this strategy succeeded. Thirdly, randomly stratified sampling was employed to examine the occurrence of juvenile abalone in three

habitats, i.e., crevices, exposed flat rocks, and exposed vertical rocks. These habitats were distinguished because they were known to be occupied by different numbers of urchins and juvenile abalone (Day and Branch 2000a). In every plot, ten 0.25 × 0.25-m quadrats were placed over each of the three habitats (thus totaling 90 quadrats per site), and juvenile abalone counted. If the habitat covered only a portion of the quadrat, counts were restricted to that habitat, and an estimate made of the percentage of the quadrat covered by that habitat. The data were then converted into numbers per unit area of the habitat in question.

Abalone recruits.—Spawning of *Haliotis midae* occurs between November and March (Newman 1967) and the effects of urchin removal on abalone recruits were monitored between December 1995 and February 1996. Although counting recruits is only a surrogate for measuring settlement, the data do record how many recruits survived, even though it is not possible to separate differential settlement and post-settlement survival. After settlement, abalone recruits remain on coralline substrata for up to eight weeks (Tarr 1989). The brevity of this window of time meant that each site could only be surveyed once. This was done as soon as recruits were detected. For each of the three treatments at all six sites, recruits were surveyed in 20 randomly placed 0.25 × 0.25-m quadrats.

Substrate effects.—Substrate cover and composition were monitored in each plot. Divers initially sampled six (and later 8–10) 0.5 × 0.5-m quadrats per plot. The quadrats were placed between 1.5 and 2.0 m apart along two weighted lines which crossed each other at right angles through the center of the circle. Where quadrats fell on >50% sand, they were moved to the closest area of rock. In each quadrat, we recorded the numbers of urchins and kelp sporlings and the percent cover of the following substrate categories: sand (always deeper than 5 cm); mats of polychaete tubes overlying rock (primarily colonies of *Paronuphis antarctica*); encrusting corallines; foliar algae; kelp holdfasts; and sponge. All of these substrata could be sampled without disturbance to the plot, and were monitored after 3 wk, after 2 mo, after 5 mo, and after 2 yr (Table 1). After the first two surveys, it became evident that two additional variables should be examined. One was the depth to which hard surfaces were covered by a fine film of sand and organic particles, hereafter referred to as sediment (when this exceeded 5 mm, the surface was recorded as sand). The other was drift kelp. A single collection of all drift kelp in each plot was performed after five months, and the drift was wet weighed.

Quantification of shelter.—Availability of shelter was measured by swimming along a weighted rope placed across the diameter of each circle and recording the lengths of three habitat types that fell directly beneath the rope. Four replicate transects were sampled per plot. The habitats distinguished were: (1) vertical

and flat exposed rock (clean rock faces that were bare or encrusted with corallines); (2) shelter (crevices or space beneath rocks); (3) unsuitable habitat (sand, shale, gravel, pebbles <10 cm, kelp holdfasts, foliar algae, mats of polychaete tubing, and the encrusting red alga *Hildenbrandia*; none of which ever supported urchins or juvenile abalone); (4) shelter beneath urchins. The shelter provided by urchins was calculated from their density and mean radius (35 mm, including their spiny canopy). Crevices were defined as sheltered areas between contiguous rocks, and cracks that were ≥5 cm deep and ≥1.5 cm wide. Surveys of shelter were undertaken both immediately before and immediately after the establishment of the different treatments in the plots.

Data analyses

Most of the data were analysed with ANOVA of various designs, preceded by Levene's test of homogeneity of variance to ensure the assumptions of ANOVA were met. When necessary, data were square-root or ARCSIN transformed to achieve normality. Tukey a posteriori tests were applied if ANOVAs revealed significant differences ($P < 0.05$).

Urchins, abalone juveniles, and recruits.—Quadrat data were converted to numbers of juvenile abalone or urchins per m² of suitable habitat (i.e., excluding unsuitable habitat). Many quadrats contained no abalone. Consequently, the data were normalized by square-root transformation (after adding 0.5 to each value to eliminate zeroes). The data were analysed separately for each time period, using two-way ANOVAs, with Treatment as a fixed effect (as it covered all three predefined treatments), and Site as a random effect (because sites represented a sample of all possible sites in the region). Quadrats were used as the unit of replication because they were randomly positioned and independent. As the quadrats were small relative to the total area of each plot, the chance of resampling the same place even on different dates was slim (<1%).

To compare distributions of juvenile abalone on different habitat types (i.e., crevices, exposed flat rock, or exposed vertical rock), quadrat data were pooled for each plot, so that sites became the unit of replication. Pooling was necessary because some of the habitats were limited in extent, thus raising the possibility that sampling on different dates could have covered the same places. In such an event, individual quadrats would not have represented truly independent samples. A three-way, repeated-measures ANOVA, with Time and fixed effects (Treatment and Habitat), was run on these data. Since only four of the six sites were monitored after 2 yr, this time period was omitted from the ANOVA. The recruit data, derived from a single sampling, were analysed using a two-way ANOVA with Treatment as a fixed effect and Sites as a random factor.

Substratum.—Percent cover data were converted into area, and then recalculated as a percentage of hard

substrate area in the quadrat (i.e., excluding areas of sand). These percentages were then ARCSIN transformed. Discrete data, such as the numbers of kelp sporlings, were square-root transformed as for juvenile abalone. Since large between-site differences existed in the mass of drift kelp, absolute masses could not be statistically compared. Instead, the weights of drift found in urchin-removal and disturbance-control plots were subtracted from that found in undisturbed control plots. The data thus obtained were compared using a one-way ANOVA. The availability of different habitat types at each site and in each treatment plot was analysed using a two-way ANOVA and ARCSIN-transformed data.

RESULTS

Densities of urchins

Initial total counts of urchins, obtained before the establishment of the treatments, were first expressed as densities for the entire area of each plot (thus including patches of unsuitable habitat such as sand, which were not sampled in subsequent surveys). Measured in this manner, urchin densities varied between 28 and 55 urchins/m^2 (Fig. 2A). Despite variability between sites, densities at each site were similar between the plots designated for undisturbed controls, disturbance-control and urchin-removal treatments.

Density data are, however, more usefully viewed per unit area of suitable (i.e., hard) substratum, measures of which were obtained from quadrat surveys within each plot (Fig. 2B). Expressed in this way, there were initially no significant differences in the density of urchins among the three types of treatment plots at any of the sites, although there was significant variation among sites (Table 2). With implementation of the experimental treatments, urchins were eliminated from the urchin-removal treatment, and few ever reinvaded. Densities of urchins in disturbance-control plots consistently remained statistically indistinguishable from those in undisturbed controls, and both had significantly more urchins than the removal plots (Table 2, Fig. 2B).

Effects of urchin removal on juvenile abalone

Data relating to juvenile abalone were similarly expressed as densities on suitable substrata, measured in quadrats (Fig. 2C, Table 2). As in the case of urchins, there was considerable variation between sites, but initially no significant within-site differences between plots designated for the three treatments. At all sites, densities of juvenile abalone declined dramatically with time after removal of urchins. Twelve hours after the initiation of the experiment, one site (Buffels-A) was surveyed, and the densities of juveniles/m^2 of suitable habitat were 8.5 (±4.31; 1 SD) in the urchin-removal plot, 24.44 (±22.76) in the disturbance-control plot, and 24.66 (±18.46) in the undisturbed control

plot. Three weeks after the experiment had begun, a full-scale survey of all sites showed that juvenile densities were significantly lower in urchin-removal plots than in disturbance-controls and undisturbed controls, which did not differ significantly from each other (Table 2). After 5 mo, and even after 2 yr, the same pattern still existed, with densities of juveniles in urchin-removal treatments having declined to almost zero.

These general results conceal, however, any potential influences of the three types of suitable habitat (crevices, exposed flat rock, or exposed vertical rock) on the extent to which abalone juveniles were affected by urchin removal. Fig. 3 illustrates the difference in numbers of juveniles found over time in each habitat, while Table 3 shows the corresponding statistical analyses. Prior to urchin removal, the densities of juvenile abalone were statistically indistinguishable between urchin-removal, undisturbed control and disturbance-control plots, irrespective of which habitat was being considered (Tukey test, $P > 0.05$). However, in all plots, the densities in crevices were significantly higher ($P < 0.05$) than those on vertical or flat rocks, between which no differences were found ($P > 0.05$). This pattern was maintained throughout the experiment in undisturbed controls and disturbance-controls, which never differed significantly. Thus, the short-term disturbance of urchins did not in itself seem to have any detectable effects on the densities of juvenile abalone in any of the habitats.

In urchin-removal treatments, crevices still maintained higher densities of juvenile abalone than other habitats when sampling took place after three weeks, by which time the only abalone remaining were those found in crevices. After five months had elapsed, no significant differences existed between any of the habitats ($P > 0.05$), reflecting the virtual absence of juvenile abalone from all of the habitats in the urchin-removal plots. Searches confirmed that the juvenile abalone had not simply moved to alternative forms of shelter after removal of the urchins. Thus, in the absence of urchins, crevices provided a temporary stay of execution for a small proportion of the juvenile abalone originally present, but failed to sustain these animals in the longer term.

Effects of urchin removal on abalone recruits

Significant effects of urchin removal were also evident on the densities of abalone recruits after 4 mo (Fig. 4). Densities in different habitats and across treatments differed significantly (ANOVA, $F_{2,20} = 4.44$, $P < 0.02$, and $F_{2,20} = 5.89$, $P < 0.01$ respectively). High variability between sites was evident, but the most striking outcome was that no recruitment occurred in the urchin-removal plots at any of the six sites. Recruits were significantly more abundant in undisturbed controls and disturbance-control plots at five of the six sites (Tukey, $P < 0.05$), but no difference existed between these two controls (Tukey, $P > 0.05$). Densities
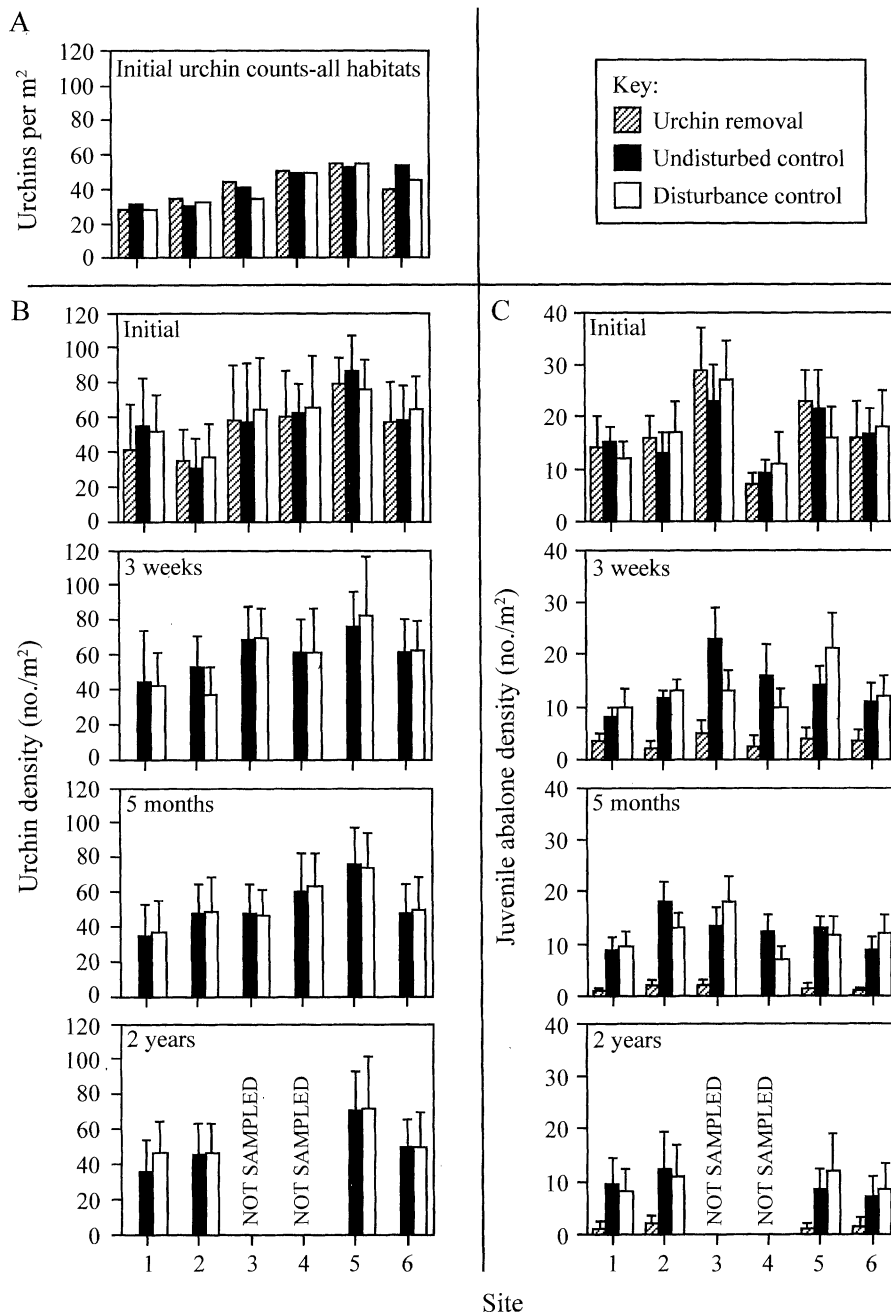
FIG. 2. Densities of urchins and juvenile abalone. (A) Initial urchin densities, across entire treatment plots. (B) Urchin densities within quadrats, on hard substrates only. (C) Densities of juvenile abalone within quadrats, on hard substrates only. For (B) and (C), the data are means taken of 10 quadrat samples per plot (+1 SD). Sites are indicated by numbers: 1, Boordjies-A; 2, Boordjies-B; 3, Buffels-A; 4, Buffels-B; 5, Millers; 6, Pyramid.

in crevices were virtually zero, and significantly lower than on flat and vertical rock (Tukey, $P < 0.05$).

Effects of substrate cover

Of all the substrate cover components analysed, the only significant differences found between treatments were for sediment and drift kelp. No treatment effects were observed in the ANOVAs at any time period for sand, polychaete mats, foliar algae, encrusting corallines, sponge, kelp holdfasts, or kelp sporlings. Consequently results for these components are not presented here. (The data are documented in Table 3.6 of Day 1998.)

No differences in sediment cover were visible between treatments at the start of the experiment, but did emerge thereafter (Fig. 5). Two-way ANOVAs showed

TABLE 2. Results of two-way ANOVAs to test for differences between densities of urchins and of juvenile abalone in different treatments and at six different sites.

Elapsed time	Effect	df	Urchins		Abalone	
			F	P	F	P
Initial	site	5, 162	5.32	<0.01	4.75	<0.005
	treatment	2, 10	0.18	>0.05	0.12	>0.05
3 weeks	site	5, 162	7.83	<0.001	2.86	<0.025
	treatment	2, 10	10.25	<0.001	22.90	<0.001
5 months	site	5, 162	6.03	<0.01	4.53	<0.001
	treatment	2, 10	9.62	<0.001	16.27	<0.001
2 years	site	3, 108	27.92	<0.001	1.35	>0.05
	treatment	2, 6	443.57	<0.001	25.88	<0.001

Notes: No interaction terms were significant. Only four sites could be sampled after two years. Results of Tukey a posteriori tests were as follows. (1) Treatment effects for both urchins and juvenile abalone: Removal < Control = Disturbance for all time periods except Initial. (2) Site effects for urchins: Millers Point had significantly more urchins than some or all of the remaining sites, which were not distinguishable at any time. (3) Site effects for abalone: Effects were detected but displayed no pattern.

significant treatment effects after both 5 mo ($F_{2,10}$ = 32.13, $P < 0.001$) and 2 yr ($F_{2,6}$ = 8.36, $P < 0.02$). At all sites, urchin-removal treatments had significantly greater amounts of sediment than other treatments (Tukey, $P < 0.05$). Despite apparent variation between sites, ANOVAs showed neither site effects nor any interaction between sites and treatments ($P > 0.05$).

Fig. 6 shows that urchin-removal plots had significantly less drift kelp than either undisturbed controls or disturbance-controls (one-way ANOVA, $F_{1,4}$ = 7.72, $P < 0.05$; Tukey test, $P < 0.05$), but the undisturbed control and disturbance-control plots were not statistically distinguishable (Tukey test, $P > 0.05$).

Availability of shelter for abalone

Initially, the availability of different habitats in different treatment plots was comparable (Table 4: ANOVA, $F_{2,10}$ = 0.0007, $P \gg 0.05$). No significant differences were found in densities of abalone juveniles occupying flat or vertical habitats (Tukey test, $P > 0.05$). Consequently, these habitats have been lumped as exposed habitats in Table 4, to contrast with the crevice habitat. If urchin cover is ignored, it is evident that a relatively small proportion of the natural habitat provided shelter for juvenile abalone ($\sim17\%$), most of the reef comprising exposed surfaces. If urchins are taken into account, however, they provided considerable additional shelter in the disturbance-controls and undisturbed controls, raising the figure to $\sim37\%$ which is roughly double that available in the urchin-removal treatments (Table 4).

DISCUSSION

Effects of urchin removal on habitat characteristics

Following the removal of urchins, the most unexpected result was the almost complete absence of responses from the algal community seen in many previous studies over similar time scales: increases in foliar algae and kelp sporlings and decreases in encrust-

ing corallines (Jones and Kain 1967, Breen and Mann 1976, Dayton 1985a, Johnson and Mann 1988, Morrison 1988, Vadas and Steneck 1995). Fricke (1979) did observe increases in sporlings of the kelps *Ecklonia maxima* and *Laminaria pallida* following urchin removal from a single unreplicated site in False Bay (close to our research sites). He attributed this response primarily to the elimination of grazing by *Parechinus angulosus*. Sporlings of these kelps occur predominantly in nurseries provided by holdfasts of adult kelps, where they are largely protected from grazing (Velimirov et al. 1977, Anderson et al. 1997). Velimirov and Griffiths (1979) observed that waves cause the long fronds of the kelp *L. pallida* to sweep the substratum around the holdfast, keeping the peripheries of the holdfast nurseries free of grazers. Holdfasts of both kelps were present in all our experimental sites, and these nurseries should thus have protected kelp sporlings equally in all treatments.

One cannot, however, assume that urchins necessarily decrease the density of kelp sporlings by grazing on them. Dayton (1985b) believes that entrapment of fertile kelp fronds by urchins can actually enhance local kelp recruitment. In our case, and contrary to our hypothesis that macroalgae would increase, the experimental removal of urchins had neither negative nor positive effects on the densities of kelp sporlings or other foliar algae. The most likely explanation for these unexpected results lies in the kelp-trapping capabilities of the urchins.

In this context, the marked reduction in drift kelp in urchin-removal plots is informative (Fig. 6). Much of the drift kelp that we sampled in undisturbed controls and disturbance-controls comprised small pieces attached to the tube feet or beneath the tests of urchins, and it appears that the urchins actively retained drift kelp in these areas. Velimirov et al. (1977) considered *P. angulosus* to be a debris feeder rather than a grazer. Dayton (1985a) has previously noted that some urchins
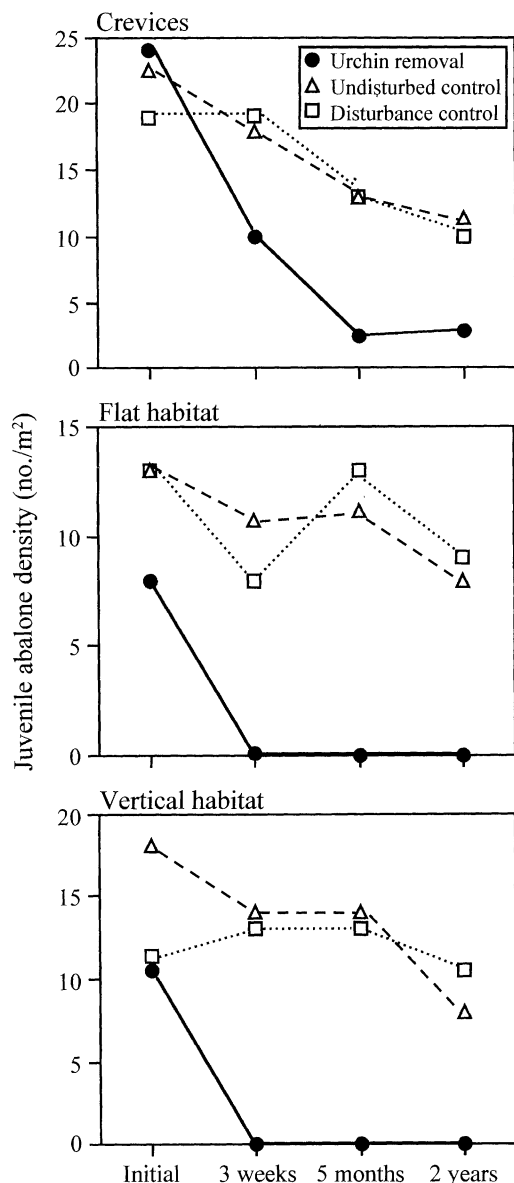
FIG. 3. Effects of urchin removal on the densities of juvenile abalone in different habitats (mean values, $n = 10$; standard deviations were too small to indicate here). Note differences in the ordinate scales.

(Lawrence and Sammarco 1982, Steinberg 1995). Some algae may even inhibit the grazing activities of urchins by way of the whiplash action of their fronds and the abrasion they cause (Velimirov and Griffiths 1979, Konar 2000).

It appears, therefore, that the unpredicted results of the grazer removal experiment reported here are due to the fact that *P. angulosus* did not act as a grazer and thus failed to exert top-down consumer effects. Tegner and Dayton (1991) noted that the critical factor driving the creation of urchin barrens is the ratio between drift availability and grazing pressure. A decrease in the former or an increase in the latter can trigger destructive overgrazing. Thus, by moderating grazing in our system, the provision of drift kelp had important indirect density-mediated effects on both foliar algae and encrusting corallines, and indirect trait-mediated effects on the juveniles of abalone, which have well-developed behavior patterns that allow them to locate and remain beneath urchins.

The only other significant effect of urchin removal on substrate cover was the increased accumulation of sediment on hard substrata. This result is not easy to explain. Kennelly (1987) found that silt accumulated on experimental plates from which grazers were excluded, and attributed this to entrapment of silt associated with increases in microalgae. Another possible explanation is that the movements of urchins, which were present in high densities, may have caused sufficient disturbance to retard sedimentation. Although drift-feeding urchins are sedentary, this mode of feeding does represent a constant source of motion at the substrate surface. A third possibility is that pieces of drift kelp trapped by the urchins have a whiplash effect, analogous to that of the fronds of living kelp described by Velimirov and Griffiths (1979). We consider this unlikely, as the mean size of the fragments trapped (~50 mm; E. Day and G. M. Branch, *personal observations*) was too small to achieve this effect. All of these explanations remain speculative. Nevertheless, even if the mechanism is an open question, the consistently higher rates of sediment accumulation observed in the six independent urchin-removal plots

trap kelp as opposed to grazing, and Duggins and Eckman (1994) have suggested that consumption of aged drift material is nutritionally superior to eating fresh kelp, which has not yet accumulated bacterial and diatom communities. Both Harrold and Reed (1985) and Tegner et al. (1995) report that in Californian kelp forests, urchins are normally sustained by drift kelp, and attack living kelp plants only when drift is limiting. Similar observations have been made in Chile by Contreras and Castilla (1987) and point to some urchins playing a substantially less important role than the "keystone grazers" they are often reputed to be

TABLE 3. Results of the three-way repeated measures ANO-VA to test for differences in densities of juvenile abalone in different habitats (crevices, flat rock, vertical rock), in different treatments, over time (replication at level of site).

Effect	Degrees of freedom	F	P
Treatment	2, 72	32.087	<0.001
Habitat	2, 72	17.688	<0.001
Time	2, 72	54.981	<0.001
Treatment × Habitat	4, 72	1.549	>0.05
Treatment × Time	4, 72	17.791	<0.001
Habitat × Time	4, 72	3.749	<0.01
Treatment × Habitat × Time	8, 72	0.645	>0.05

Note: Data are from first five months only.
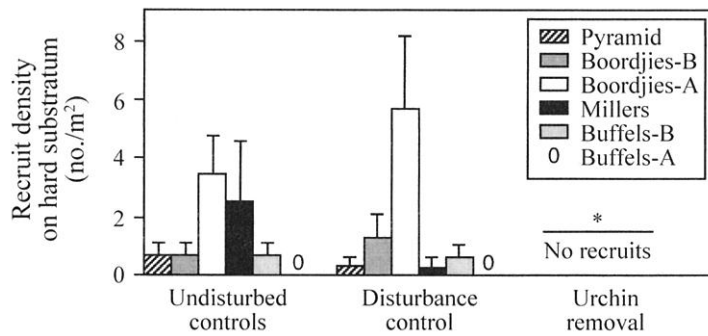
E. DAY AND G. M. BRANCH

FIG. 4. The effect of urchin removal on abalone recruits (mean + 1 SD; $n = 20$) at six sites. The asterisk indicates results that were significantly different from other treatments. No recruits were recorded in any of the treatments at one of the sites (Buffels-A).

(Fig. 5) clearly indicate sedimentation was influenced by the presence of urchins. In the long term, this may be a highly significant effect, possibly contributing to the prevalence of mats of polychaete tubes observed in certain habitats formerly dominated by urchins (see Day and Branch 2000a).

Effects of urchin removal on abalone recruits

Recruitment of abalone occurred in all disturbance-controls and undisturbed controls, except at Buffels-A, where no recruits were detected anywhere. In contrast, recruits were absent from urchin-removal plots at all six sites (Fig. 4). The absence of recruits from urchin-removal plots was surprising, because earlier recruit surveys (Day and Branch 2000b) showed that the association between abalone recruits and urchins is considerably weaker than that existing between abalone juveniles and urchins. Thus, whereas urchin removal was expected to negatively affect juveniles, survival of recruits was not considered critically dependent on the presence of urchins. We had hypothesized that urchins might indirectly benefit recruits by preventing the overgrowth of encrusting corallines by macroalgae, as Fletcher (1987) recorded in Australia. However, neither macroalgal cover nor encrusting corallines responded to the removal of urchins, so this hypothesis was falsified in our system.

The significant increase in sediment in urchin-re-

moval treatments provides a more plausible explanation. Andrew and Choat (1985) remarked that juvenile urchins are vulnerable to smothering by silt, and Tegner and Butler (1989) observed that the highest densities of very small juveniles of Haliotis rufescens (<5 mm) are found on silt-free substrata, and that they generally do not attach well to silty surfaces. Saito (1981) corroborated such findings. Thus, the effect of urchins on rates of sedimentation may indirectly impact abalone recruits.

There are, however, other feasible explanations for the disappearance of recruits from urchin-removal plots. In aquaculture tanks, Matthews and Cook (1995) found that grazed substrata support a diatom community dominated by prostrate genera, which appear more suitable for abalone settlement than those communities that thrive in the absence of grazers. Thus, substrate grazing by urchins may benefit abalone settlement processes (Slattery 1992). If so, an absence of urchins could be of major importance to recruits, since they are initially entirely reliant on the food supply available on coralline surfaces (Kawamura et al. 1995). However, this argument is compromised by the fact that where we worked, Parechinus angulosus appeared to be a drift collector rather than a grazer, and thus is unlikely to alter the substrate composition by grazing. Other grazers, unaffected by the urchin-removal experiment, may of course play a role in preventing the overgrowth
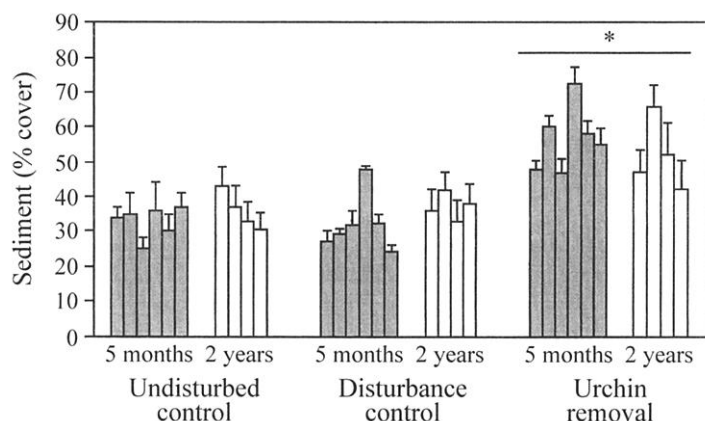

FIG. 5. The effect of urchin removal on sediment percentage cover (mean + 1 SD; $n = 8$–10) at six sites. The asterisk denotes results that are significantly different from other treatments. Only four of the six sites (white bars) could be sampled after two years; Boordjiesrif-A and Boordjiesrif-B were not sampled after two years. Bars show data from sites in the following order (left to right): Millers Point, Pyramid Rock, Boordjiesrif-A, Boordjiesrif-B, Buffels Bay-A, and Buffels Bay.

Fig. 6. The effect of urchin removal on accumulation of drift kelp at five sites (one of the six sites, Buffels-A, could not be sampled). The asterisk indicates results that are significantly different from other treatments. Each result is the total biomass for an entire plot.
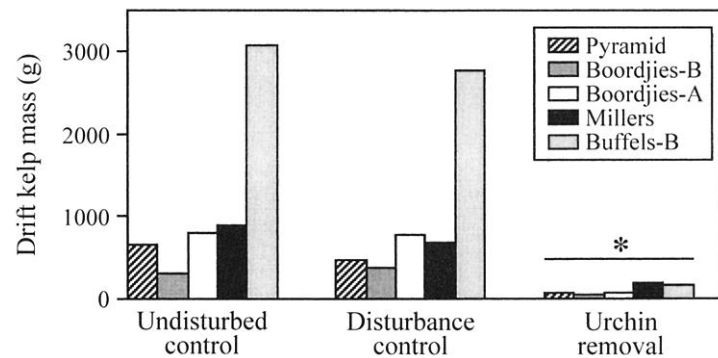
of corallines. Additionally, the encrusting corallines themselves may prevent overgrowth and fouling by sloughing their surface layers (Johnson and Mann 1986, Keats et al. 1994).

The results of the removal experiments have clarified one question raised during earlier field surveys (Day and Branch 2000b). Some urchins have negative effects because their coarse-grained method of grazing over the substratum can bulldoze small underlying invertebrates, including abalone recruits (Andrew and Underwood 1992, McShane 1992). This leads to the logical prediction that recruit survival should be enhanced in the absence of urchins, whereas we recorded the opposite. This apparent contradiction is explicable. If *P. angulosus* does not act as a grazer, the threat of recruits being bulldozed by it should be negligible. Both Harrold and Reed (1985) and Tegner (1989) found that urchin movements are considerably decreased when they feed by collecting drift. In our case, low mobility was observed year-round. The need to maintain urchin removals during our experiment was minimal, and urchin-removal plots revisited two years after treatments began were still virtually free of urchins. Under such conditions of low urchin movement, abalone recruits that shelter under urchins probably gain relatively permanent protection from other grazers.

Effects of urchin removal on abalone juveniles

Unequivocal reductions were observed in the densities of abalone juveniles in urchin-removal treatments (Fig. 2), and it seems indisputable that their commensalism with urchins is vital for the survival of juvenile abalone. This conclusion is bolstered by large-scale field surveys, which demonstrated that 97% of the juvenile abalone were associated with urchins, and that without exception those <20 mm in length occurred beneath urchins (Day and Branch 2000a). Further support comes from the disappearance of juvenile abalone from areas in which urchin populations have collapsed (Tarr et al. 1996). Moreover, since no significant differences in abalone numbers were observed between disturbance-controls and undisturbed controls, the decline in juveniles following urchin removal cannot be attributed to any disturbance effects during the establishment of urchin-removal treatments.

At least in the short term, the impacts of urchin removal on juvenile abalone seemed to be mediated by habitat. Juvenile abalone in crevices survived for longer periods than did abalone on exposed substrata (Fig. 3). This result is intuitive, given that crevices supply a degree of shelter to juveniles. Despite this shelter, within 5 months virtually all juveniles had disappeared

TABLE 4. Percent cover of habitats in different treatment plots: (A) cover in each treatment, recorded just before removal of urchins from the removal plots, and considering only shelter provided by crevices and under boulders; (B) cover in each treatment, recorded just after treatments were initiated, and when shelter provided by urchins is additionally taken into account.

Period	Treatment	Sheltered habitat (%)	Exposed habitat (%)	Unsuitable habitat (%)
A) Before	removal	18 (9)	71 (5)	10 (3)
	control	16 (7)	68 (7)	12 (6)
	disturbance	19 (5)	70 (6)	11 (3)
B) After	removal	17 (9)	71 (6)	10 (4)
	control	37 (7)	52 (7)	10 (5)
	disturbance	37 (5)	51 (6)	11 (3)

Notes: Data are expressed as means (with 1 SD in parentheses); data are rounded to the nearest whole percentage, and sites are pooled.

from exposed habitats in urchin-removal plots at all six sites, and even in crevices, numbers were down to 14% of those in undisturbed controls and disturbance controls (Fig. 3). Because the densities of juvenile abalone in crevices declined in urchin-removal plots relative to those in both types of control plots, we are confident that the juveniles did not simply move to alternative sources of shelter when urchins were removed. Had they done so, their densities in crevices should have risen in urchin-removal plots, rather than declining. Their rapid decline in crevices also indicates that crevices were on their own incapable of matching the level of protection provided by urchins.

Shelter plays an important role in the survival of the juveniles of other invertebrate species, which suffer higher predation rates when crevices are limited (Nelson and Vance 1979, Andrew 1989). In the present study, urchins themselves contributed over half the available shelter (Table 4), and were distributed across the whole reef, occupying both exposed and sheltered habitats. Their occurrence in exposed habitats is probably facilitated by the presence of the kelp forest itself, which dampens the effects of wave action (Velmirov et al. 1977). In more wave-beaten habitats, both Shepherd (1973) and Farquhar (1994) found that urchins were restricted to crevices and holes.

The disappearance of juvenile abalone from urchin-removal treatments is probably largely due to predation. Known predators of juvenile abalone include octopus (Smith 1999), the rock lobster *Jasus lalandii* (Mayfield and Branch 2000), and a range of predatory fishes (Nepgen 1982). Klipfish (*Clinus* spp.) were observed feeding on juvenile abalone after the removal of urchins. Attributing the disappearance of juvenile abalone to predators does, of course, assume that the reductions in abalone numbers reflect mortalities within the treatment plots, and not emigration from them. Given the size of the experimental plots, the rapid reduction in abalone juveniles (within 12 h at the one site monitored immediately after treatment), and the almost complete synchrony of their disappearance, emigration appears an unlikely explanation, although we cannot rule it out completely.

A remaining question concerns the potential mechanisms by which juveniles of *H. midae* benefit from their commensalism with *P. angulosus*. Apart from reducing predation on juvenile abalone, urchins might also contribute to their survival or enhanced growth in other, less direct ways. First, the distribution of urchins across a wider area than that covered by physical shelter such as crevices might disperse abalone juveniles more evenly around the reef, thereby more uniformly distributing their grazing and increasing access to food. Second, it has been hypothesized that juvenile abalone sheltering under urchins may supplement their diet by using kelp trapped by the urchins (Tegner and Levin 1982, McCormick et al. 1994). Since *P. angulosus* appeared to feed predominantly on drift kelp at our sites,

juvenile abalone sheltering beneath them might reap this advantage. If juvenile abalone can feed beneath urchins, either on drift kelp caught by the urchins or on the substratum beneath the urchins, they may reduce or even eliminate their exposure to predators while grazing. They have, in theory, obtained the perfect mobile shelter under which to feed. By contrast, in the absence of urchins, juveniles may be forced to expose themselves to predation while feeding. The fact that microalgal productivity in shaded crevices is low (<10% of that on exposed surfaces: Day 1998) reinforces that argument, implying that grazers must leave such shelters to feed.

Even if abalone under urchins do not feed directly on trapped drift kelp, the fact that the urchins are feeding on drift means that the substratum beneath urchins or in their vicinity should be grazed less than if the urchins obtain all their food by actively grazing. Indeed, for species of urchins that do not feed primarily by trapping algal debris, Andrew and Underwood (1992) remark that intense grazing by the urchins denies abalone access to food. Shepherd (1973) suggests that competition from urchins may well be a threat to the abalone resource, since they share the same food. Lowry and Pearse (1973) also hypothesize competition between urchins and abalone. In our system, however, it appears improbable that competition is an issue, since *P. angulosus* trapped drift kelp. Removal of urchins led to dramatic declines in juvenile abalone, and not the increases that would be predicted if competition occurs between them. Although not tested in our experiment, it seems unlikely that the relationship has a negative impact on the urchins, despite observations by Tegner and Levin (1982) of Californian urchins trying (albeit unsuccessfully) to prevent juvenile abalone from crawling beneath them. Given the small size and low densities of juvenile *H. midae,* it is unlikely that they adversely affect *P. angulosus*. Thus, the interaction seems to be truly commensal.

Broader implications

Our findings reach beyond the interaction of urchins and abalone. *Haliotis midae* is commercially exploited (Tarr 1989), and urchins play a pivotal role in the survival of juvenile abalone. Kelp, which is central to the interaction, is also harvested (though not where we worked). Rock lobsters, another important commercial species, consume urchins, and their increase in the area that forms the heart of the South African abalone industry has been implicated in the collapse of urchins and the disappearance of juvenile abalone (Tarr et al. 1996).

There are also broad ecological implications to our findings. Kelp is highly productive on the southwest coast of South Africa (Branch and Griffiths 1988), yet surprisingly little is consumed by active grazers (~1.4%). About 4% is eaten by drift feeders within the kelp beds, notably *P. angulosus*. Similar proportions

are stranded on adjacent rocky shores and beaches (Newell et al. 1982, Branch and Griffiths 1988). Although modest in proportional terms, this input transforms the dynamics of the recipient systems, by subsidizing the infauna of beaches (Griffiths et al. 1983) and rocky-shore filter feeders, which derive 60–79% of their food from this source (Bustamante and Branch 1996). More pertinent is the impact of drift kelp on intertidal rocky-shore herbivores. Intertidal primary productivity is high on the west coast of South Africa. In parallel, the biomass of intertidal grazers is exceptionally high (Bustamante et al. 1995). However, both modeling (Bustamante et al. 1994) and field experiments (Bustamante et al. 1996) demonstrate that subsidization by drift kelp or fronds from adjacent stands of kelp is essential to meet the energy budgets of these grazers. Sustained by inputs of kelp, these densely packed grazers exert a strong top-down effect, virtually eliminating foliar algae and often promoting monocultures of encrusting corallines. This contrasts with the situation described here for urchins, which are fueled in the same way by drift kelp, but had no discernible influence on algal community structure. As a consequence, the dramatic cascading effects on algae wrought in some North American marine communities by changes in the densities of urchins following alterations of predation intensity (Estes and Palmisano 1974, Vadas and Steneck 1995) are unlikely to occur in our system.

A different issue relating to the top-down effects of predation is whether human exploitation of top predators has changed the nature of the system with which we worked. Estes and Steinberg (1988) and Steinberg et al. (1995) have argued that benthic predators are less important in southern than in northern hemisphere kelp forests, but several important predators do occur in South African kelp beds (Field et al. 1980). Known predators of *P. angulosus* include the rock lobster *Jasus lalandii* (Mayfield and Branch 2000) and several sparid fishes, including red stumpnose *Chrysoblepharis gibbiceps,* Roman *C. laticeps,* white stumpnose *Rhabdosargus globiceps,* and hottentot *Pachymetopon blochii* (Nepgen 1982). All have been substantially depleted by 85–95% (Griffiths and Branch 1997, Attwood and Farquhar 1999, Griffiths 2000).

Regarding the ecosystem effects of depleting the sparid fishes, no more than speculation is possible; but in the case of rock lobsters, four sources of information allow an informed assessment. First, Branch et al. (1987) review how dense populations of rock lobsters produce benthic communities radically different from those that develop in the absence of rock lobsters. When lobsters are abundant, mussels, whelks, urchins, and other grazers are virtually eliminated. Instead, kelps and other foliar algae proliferate. The reverse is true in the absence of rock lobsters (Barkai and McQuaid 1988). Second, rock lobsters have recently increased at the southeastern edge of their range. Con-

comitantly, urchin populations and juvenile abalone have crashed and are nearly extinct locally (Tarr et al. 1996). Third, only rock lobsters >68 mm in carapace length are capable of eating urchins, and a negative correlation exists between the densities of urchins and rock lobsters of this size (Mayfield and Branch 2000). Fourth, evidence from archeological middens on the west coast of South Africa indicates that modal sizes of prehistorically harvested *Jasus lalandii* were as much as 116 mm in carapace length, in deposits 10 000 yr old (A. Jerardino, *personal communication*). In modern catches, animals of that size would now be regarded as rare exceptions.

These four lines of evidence all infer that reductions in the density or size of rock lobsters due to human exploitation could have significantly reduced predation on urchins, leading to increases in their density. This outcome would have enhanced the protection urchins provide juvenile abalone, especially in years of high abalone recruitment when the availability of urchins becomes limiting (Mayfield and Branch 2000). These inferences are strong, but the absence of baseline data prevents unequivocal conclusions.

Parallel situations have been documented elsewhere and are reviewed by Tegner and Dayton (2000). Elimination of sea otters from parts of the United States and Canada caused increases in urchins and declines in kelp (Estes and Palmisano 1974). The creation of a fully protected marine reserve in New Zealand led to increases in rock lobsters (*Jasus edwardsii*) and a predatory sparid fish (*Pagrus auratus*), declines in urchins, and a shift of algal community structure from encrusting coralline barrens to kelps and fucoids (Babcock et al. 1999).

Conclusions

As summarized in Fig. 7, our experiments have shown that juveniles of *H. midae* depend heavily on their commensal association with urchins. The primary role of the urchins is most likely to provide protection against predators, thus moderating top-down effects. The urchins may also influence trophic relationships by supplementing the diet of juvenile abalone. Abalone recruits likewise survived only in those areas in which urchins were present, in spite of the fact that correlations from field data inferred a weak relationship between the recruits and urchins (Day and Branch 2000*b*). This effect on recruits is tentatively attributed to the increased sedimentation that followed removal of urchins, although the exact mechanism has yet to be established. Urchin removal also resulted in a dramatic decrease in the accumulation of drift kelp. Drift kelp is clearly an important food resource for *P. angulosus,* and this fact may explain the startling lack of any response by algal communities following urchin removal. Not only did encrusting corallines fail to show any of the predicted fouling effects following the removal of
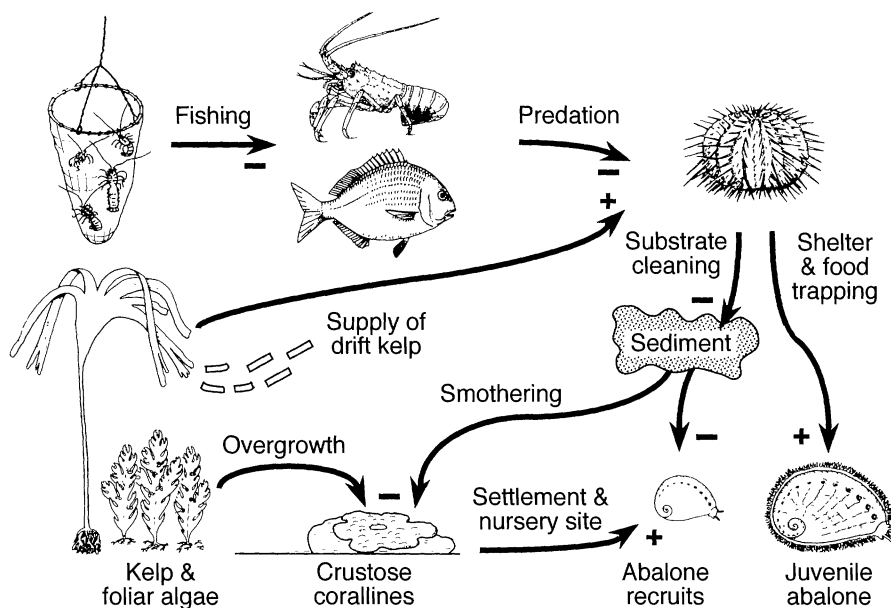
FIG. 7. Summary of the experimental results in the context of the regional interaction web, showing the crucial direct and indirect effects of urchins on the recruitment and survival of abalone. Arrows point to the species positively (+) or negatively (−) affected by the interactions.

P. angulosus, but also no increases in macroalgae were observed.

Of the five hypotheses advanced in the *Introduction,* two were confirmed (one for reasons different from those originally advanced), and three were rejected. (1) As predicted, juvenile abalone clearly depended heavily on the presence of urchins, and their decline began immediately after removal of urchins. (2) Contrary to our hypothesis, abalone recruits seemed equally dependent on urchins. (3) *P. angulosus* could not on its own control macroalgal growth and its removal had no effect on algal standing stocks or community structure, probably because these urchins depended on kelp drift rather than being active grazers. (4) Removal of urchins did not reduce coralline algae. (5) Recruitment of abalone ceased in urchin-removal plots, not because of the postulated decline in encrusting corallines, but possibly because of increased sedimentation.

Our results demonstrate important ecosystem effects that depend upon positive interactions between species, indirect effects, and an interplay between bottom-up subsidies and top-down predation. The tangled web of interactions between species, many of which are commercially exploited, exemplifies both the importance of experimental work to clarify their nature, and the need for an ecosystem approach to fisheries management to complement the traditional single-species approach (Larkin 1996, Tegner and Dayton 1999).

LITERATURE CITED

Abrams, P., B. A. Menge, G. G. Mittelbach, D. Spiller, and P. Yodzis. 1996. The role of indirect effects in food webs. Pages 371–394 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman Hall, New York, New York, USA.

Anderson, R. J., P. Carrick, G. J. Levitt, and A. Share. 1997. Holdfasts of adult kelp *Ecklonia maxima* provide refuges from grazing for recruitment of juvenile kelps. Marine Ecology Progress Series **159**:265–273.

Andrew, N. L. 1989. Contrasting ecological implications of food limitation in sea urchins and herbivorous gastropods. Marine Ecology Progress Series **51**:189–193.

Andrew, N. L., and J. H. Choat. 1985. Habitat related differences in the survivorship and growth of juvenile sea urchins. Marine Ecology Progress Series **127**:155–161.

Andrew, N. L., and A. J. Underwood. 1992. Associations and abundance of sea urchins and abalone on shallow subtidal reefs in southern New South Wales. Australian Journal of Marine and Freshwater Research **43**:1547–1559.

Attwood, C. D., and M. Farquhar. 1999. Collapse of linefish stocks between Cape Hangklip and Walker Bay, South Africa. South African Journal of Marine Science **21**:415–433.

Ayling, A. M. 1981. The role of biological disturbance in temperate subtidal encrusting communities. Ecology 62: 830–847.

Babcock, R. C., S. Kelly, N. T. Shears, J. M. Walker, and T. J. Willis. 1999. Changes in community structure in marine reserves. Marine Ecology Progress Series 189:125–134.

Barkai, A., and C. D. McQuaid. 1988. Predator–prey role reversal in a marine benthic ecosystem. Science 242:62–64.

Benedetti-Cecchi, L., F. Bulleri, and F. Cinelli. 1998. Density dependent foraging of sea urchins in shallow subtidal reefs on the west coast of Italy (western Mediterranean). Marine Ecology Progress Series 163:203–211.

Bernstein, B. B., B. E. Williams, and K. H. Mann. 1981. The role of behavioural responses to predators in modifying urchins' (Strongylocentrotus droebachiensis) destructive grazing and seasonal foraging patterns. Marine Biology 63:39–49.

Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. Trends in Ecology and Evolution 9:191–193.

Branch, G. M., A. Barkai, P. A. R. Hockey, and L. Hutchings. 1987. Biological interactions: causes or effects of variability in the Benguela ecosystem. South African Journal of marine Science 5:425–445.

Branch, G. M., and C. L. Griffiths. 1988. The Benguela ecosystem. Part V. The coastal zone. Oceanography and Marine Biology Annual Review 26:395–486.

Branch, G. M., and C. A. Moreno. 1994. Intertidal and subtidal grazers. Pages 75–100 in W. R. Siegfried, editor. Rocky shores: exploitation in Chile and South Africa. Ecological studies. Volume 103, Springer-Verlag. Berlin, Germany.

Breen, P. A., W. Carolsfeld, and L. K. Yamanaka. 1985. Social behaviour of juvenile red sea urchins, Strongylocentrotus franciscanus (Agassiz). Journal of Experimental Marine Biology and Ecology 92:45–61.

Breen, P. A., and K. H. Mann. 1976. Destructive grazing of kelp by sea urchins in Eastern Canada. Journal of the Fisheries Research Board of Canada 33:1278–1283.

Bustamante, R. H., and G. M. Branch. 1996. The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. Journal of Experimental Marine Biology and Ecology 196:1–28.

Bustamante, R. H., G. M. Branch, and S. Eekhout. 1996. Maintenance of an exceptional intertidal grazer biomass: subsidy by subtidal kelps. Ecology 76:2314–2329.

Bustamante, R. H., G. M. Branch, S. Eekhout, B. Robertson, P. Zoutendyk, M. Schleyer, A. Dye, N. Hanekom, D. Keats, M. Jurd, and C. D. McQuaid. 1995. Gradients of intertidal primary productivity around the coast of South Africa and their relationship with consumer biomass. Oecologia (Berlin) 102:189–201.

Bustamante, R. H., W. M. Getz, and G. M. Branch. 1994. Analyses of a limpet fishery using a metaphysiological stand-growth model. Natural Resources Modeling 8:139–161.

Camus, P. A. 1994. Recruitment of the intertidal kelp Lessonia nigrescens Bory in northern Chile: successional constraints and opportunities. Journal of Experimental Marine Biology and Ecology 184:171–181.

Castilla, J. C., and C. A. Moreno. 1982. Sea urchins and Macrocystis pyrifera: Experimental test of their ecological relations in southern Chile. Pages 257–263 in J. M. Lawrence, editor. Proceedings of the International Echinoderms Conference (Tampa Bay). A. A. Balkema, Rotterdam, The Netherlands.

Contreras, S., and J. C. Castilla. 1987. Feeding behaviour and morphological adaptations in two sympatric sea urchin species in central Chile. Marine Ecology Progress Series 38:217–224.

Day, E. 1998. Ecological interactions between abalone (Haliotis midae) juveniles and sea urchins (Parechinus angulosus), off the South-west coast of South Africa. Dissertation. University of Cape Town, Cape Town, South Africa.

Day, E., and G. M. Branch. 2000a. Field evidence for an association between juveniles of the South African abalone Haliotis midae and the sea urchin Parechinus angulosus. South African Journal of Marine Science 22:137–144.

Day, E., and G. M. Branch. 2000b. Relationships between recruits of the abalone Haliotis midae, encrusting corallines and the sea urchin Parechinus angulosus. South African Journal of Marine Science 22:145–156.

Dayton, P. K. 1985a. The structure and regulation of some South American kelp communities. Ecological Monographs 55:447–468.

Dayton, P. K. 1985b. Ecology of kelp communities. Annual Review of Ecology and Systematics 16:215–245.

Dethier, M. N., and D. O. Duggins. 1984. An "indirect commensalism" between marine herbivores and the importance of competitive hierarchies. American Naturalist 124:205–219.

Duggins, D. O., and J. E. Eckman. 1994. The role of kelp detritus in the growth of benthic suspension feeders in an understory kelp forest. Journal of Experimental Marine Biology and Ecology 176:53–68.

Ebeling, A. W., D. W. Laur, and R. J. Rowley. 1985. Severe storm disturbances and reversal of community structure in a southern California kelp forest. Marine Biology 84:287–294.

Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in the structuring of nearshore communities. Science 185:1058–1060.

Estes, J. A., and P. D. Steinberg. 1988. Predation, herbivory and kelp evolution. Paleobiology 14:19–36.

Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters: linking oceanic and nearshore ecosystems. Science 282:473–476.

Farquhar, M. R. 1994. Interspecific interactions of the sea urchin Parechinus angulosus and the effect of variation in microhabitat availability. Thesis. Rhodes University, Grahamstown, South Africa.

Field, J. G., C. L. Griffiths, R. J. Griffiths, N. Jarman, P. Zoutendyk, B. Velimirov, and A. Bowes. 1980. Variation in structure and biomass of kelp communities along the south-west Cape Peninsula. Transactions of the Royal Society of South Africa 44:145–203.

Fletcher, W. J. 1987. Interactions among subtidal Australian sea urchins, gastropods, and algae. Effects of experimental removals. Ecological Monographs 57:89–109.

Fricke, A. H. 1979. Kelp grazing by the common sea urchin Parechinus angulosus Leske in False Bay, Cape. South African Journal of Zoology 14:143–148.

Griffiths, C. L., and G. M. Branch. 1997. The exploitation of coastal invertebrates and seaweeds in South Africa: historical trends, ecological impacts and implications for management. Transactions of the Royal Society of South Africa 52:121–148.

Griffiths, C. L., J. M. E. Stenton-Dozey, and K. Koop. 1983. Kelp wrack and the flow of energy through a sandy beach ecosystem. Pages 547–556 in A. McLachlan and T. Erasmus, editors. Sandy beaches as ecosystems. W. Junk, The Hague, The Netherlands.

Griffiths, M. 2000. Long-term trends in catch and effort of commercial linefish of South Africa's Cape Province: snapshots of the 20th century. South African Journal of Marine Science 22:81–110.

Hagen, N. T. 1995. Recurrent destructive grazing of successionally immature kelp forests by green sea urchins in

E. DAY AND G. M. BRANCH

Vestfjorden, Northern Norway. Marine Ecology Progress Series **123**:95–106.

Hairston, N. G., Jr., and N. G. Hairston, Sr. 1993. Does food-web complexity eliminate trophic-level dynamics? American Naturalist **149**:1001–1007.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist **94**:421–425.

Harrold, C., and J. S. Pearse. 1987. The ecological role of echinoderms in kelp forests. Echinoderm Studies **2**:137–233.

Harrold, C., and D. C. Reed. 1985. Food availability, sea urchin grazing, and kelp forest community structure. Ecology **66**:1160–1169.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology **12**:197–229.

Johnson, C. R., and K. H. Mann. 1986. The crustose coralline alga *Phymatolithon* Foslie, inhibits the overgrowth of seaweeds without relying on herbivores. Journal of Experimental Marine Biology and Ecology **96**:127–146.

Johnson, C. R., and K. H. Mann. 1988. Diversity, patterns of adaptation, and stability of Nova Scotia kelp beds. Ecological Monographs **58**:129–154.

Jones, N. S., and J. M. Kain. 1967. Subtidal algal colonisation following the removal of *Echinus*. Helgolander wissenschaftliche Meeresuntersuchungen **15**:460–466.

Kawamura, T., T. Saido, T. Takami, and Y. Yamashita. 1995. Dietary value of benthic diatoms for the growth of post-larval abalone *Haliotis discus hannai*. Journal of Experimental Marine Biology and Ecology **194**:189–199.

Keats, D. W., P. Wilson, and G. Maneveldt. 1994. Ecological significance of deep-layer sloughing in the eulittoral zone coralline alga, *Spongites yendoi* (Foslie) Chamberlain (Corallinaceae, Rhodophyta) in South Africa. Journal of Experimental Marine Biology and Ecology **175**:145–154.

Kennelly, S. J. 1987. Physical disturbances in an Australian kelp community. Temporal effects. Marine Ecology Progress Series **40**:145–153.

Konar, B. 2000. Seasonal inhibitory effects of marine plants on sea urchins: structuring communities the algal way. Oecologia (Berlin) **125**:208–217.

Larkin, P. A. 1996. Concepts and issues in marine ecosystem management. Review of Fish Biology and Fisheries **6**:139–164.

Lawrence, J. M. 1975. On the relationship between marine plants and sea urchins. Oceanography and Marine Biology Annual Review. **13**:213–286.

Lawrence, J. M., and P. W. Sammarco. 1982. The ecological effects of feeding Echinoidea. Pages 499–519 *in* M. Jangoux and J. M. Lawrence, editors. Echinoderm nutrition. A. A. Balkema, Rotterdam, The Netherlands.

Lowry, L. F., and J. S. Pearse. 1973. Abalones and sea urchins in an area inhabited by sea otters. Marine Biology **23**:213–219.

Matthews, I., and P. A. Cook. 1995. Diatom diet of abalone post-larvae (*Haliotis midae*) and the effect of pre-grazing the diatom overstorey. Marine and Freshwater Research **46**:545–548.

Mayfield, S., and G. M. Branch. 2000. Interrelations among rock lobsters, sea urchins and juvenile abalone: implications for community management. Canadian Journal of Fisheries and Aquatic Science **57**:2175–2185.

McCormick, T. B., K. Herbinson, T. S. Mill, and J. Altick. 1994. A review of abalone seeding, possible significance and a new seeding device. Bulletin of Marine Science **55**:680–693.

McShane, P. E. 1992. Early life history of abalone: a review. Pages 120–138 *in* S. A. Shepherd, M. J. Tegner, and S. A.

Guzman, editors. Abalone of the world. Biology, fisheries and culture. Fishing News Books, Oxford, UK.

Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. Ecological Monographs **65**:21–74.

Menge, B. A. 1997. Detection of direct versus indirect effects: were experiments long enough? American Naturalist **149**:801–823.

Menge, B. A. 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. Journal of Experimental Marine Biology and Ecology **250**:257–289.

Menge, B. A., B. A. Daley, J. Lubchenco, E. Sanford, E. Dahlhoff, P. M. Halpin, and J. L. Burnaford. 1999. Top-down and bottom-up regulation of New Zealand rocky intertidal communities. Ecological Monographs **69**:297–330.

Morrison, D. 1988. Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. Ecology **69**:1367–1382.

Nelson, B. V., and R. R. Vance. 1979. Diel foraging patterns of the sea urchin *Centrostephanus coronatus* as a predator avoidance strategy. Marine Biology **51**:251–258.

Nepgen, C. S. de V. 1982. Diet of predatory and reef fish in False Bay and possible effects of purse seining on their food supply. Fisheries Bulletin of South Africa **16**:75–93.

Newell, R. C., J. G. Field, and C. L. Griffiths. 1982. Energy balance and significance of micro-organisms in a kelp bed community. Marine Ecology Progress Series **8**:103–113.

Newman, G. 1967. Reproduction of the South African abalone *Haliotis midae*. Division of Sea Fisheries, South Africa, Investigational Report 64.

Persson, L., J. Bengtsson, B. A. Menge, and M. E. Power. 1996. Productivity and consumer regulation: concepts, patterns, and mechanisms. Pages 396–434 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Pimm, S. L. 1991. The balance of nature? University of Chicago Press, Chicago, Illinois, USA.

Polis, G. A., and D. Strong. 1996. Food web complexity and community dynamics. American Naturalist **147**:813–846.

Prince, J. 1995. Limited effects of the sea urchin *Echinometra matthaei* (de Blainville) on the recruitment of benthic algae and macroinvertebrates into intertidal rock platforms at Rottnest Island, western Australia. Journal of Experimental Marine Biology and Ecology **186**:237–258.

Saito, K. 1981. The appearance and growth of 0-year Ezo abalone. Bulletin of the Japanese Society of Science and Fisheries **47**:1393–1400.

Sala, E., C. F. Boudouresque, and M. Harmelin-Vivien. 1998. Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. Oikos **83**:425–439.

Shepherd, S. A. 1973. Competition between sea urchins and abalone. Australian Fisheries (June 1973) **8**:4–7.

Slattery, M. 1992. Larval settlement and juvenile survival in the red abalone (*Haliotis rufescens*): an examination of inductive cues and substrate selection. Aquaculture **102**:143–153.

Smith, C. 1999. Population biology and ecology of octopuses in the south western Cape: a study towards the establishment of a small-scale octopus fishery. Thesis. University of Cape Town, Cape Town, South Africa.

Steinberg, P. D. 1995. Interactions between the canopy dwelling echinoid *Holopneustes purpurescens* and its host kelp *Ecklonia radiata*. Marine Ecology Progress Series **127**:169–181.

Steinberg, P. D., J. A. Estes, and F. C. Winter. 1995. Evolutionary consequences of food chain length in kelp forest communities. Proceedings of the National Academy of Sciences (USA) **92**:8145–8151.

Tarr, R. J. Q. 1989. Abalone. Pages 62–69 *in* A. I. L. Payne and R. J. M. Crawford, editors. Oceans of life off southern Africa. Vlaeberg, Cape Town, South Africa.

Tarr, R. J. Q., P. V. G. Williams, and A. J. MacKenzie. 1996. Abalone, sea urchins and rock lobster: a possible ecological shift may affect traditional fisheries. South African Journal of Marine Science 17:319–323.

Tegner, M. J. 1989. The feasibility of enhancing red sea urchin, *Strongylocentrotus franciscanus,* stocks in California: an analysis of the options. Marine Fisheries Review 51:1–22.

Tegner, M. J., and R. A. Butler. 1989. Abalone seeding. Pages 157–182 *in* K. O'Hahn, editor. Handbook of culture of abalone and other marine gastropods. CRC, Boca Raton, Florida, USA.

Tegner, M. J., and P. K. Dayton. 1977. Sea urchin recruitment patterns and implications of commercial fishing. Science 196:324–326.

Tegner, M. J., and P. K. Dayton. 1991. Sea urchins, El Ninos and the long-term stability of Southern California kelp forest communities. Marine Ecology Progress Series 77:49–63.

Tegner, M. J., and P. K. Dayton. 1999. Ecosystem effects of fishing. Trends in Ecology and Evolution 14:261–262.

Tegner, M. J., and P. K. Dayton. 2000. Ecosystem effects of fishing in kelp forest communities. ICES (International Council for Exploration of the Sea) Journal of Marine Science 57:579–589.

Tegner, M. J., P. K. Dayton, P. B. Edwards, and K. L. Riser. 1995. Sea urchin cavitation of giant kelp (*Macrocystis pyrifera* C. Agardh) holdfasts and its effects on kelp mortality across a large California forest. Journal of Experimental Marine Biology and Ecology 191:83–99.

Tegner, M. J., and L. A. Levin. 1982. Do sea urchins and abalones compete in California kelp forest communities? Pages 265–271 *in* J. M. Lawrence, editor. Proceedings of the International Echinoderms Conference (Tampa Bay). A. A. Balkema, Rotterdam, The Netherlands.

Tegner, M. J., and L. A. Levin. 1983. Spiny lobsters and sea urchins: analysis of a predator–prey interaction. Journal of Experimental Marine Biology and Ecology 73:125–150.

Vadas, R. L., and R. W. Elner. 1992. Plant–animal interactions in the north-west Atlantic. Pages 33–60 *in* D. M. John, S. J. Hawkins, and J. H. Price, editors. Plant–animal interactions in the marine benthos. Systematics Association Special Volume 46. Clarendon, Oxford, UK.

Vadas, R. L., and R. S. Steneck. 1995. Overfishing and inferences in kelp–sea urchin interactions. Pages 509–524 *in* H. R. Skjoldal, C. Hopkins, K. E. Erikstad, and H. P. Leinaas, editors. Ecology of fjords and coastal waters. Elsevier Science, Amsterdam, The Netherlands.

Velimirov, B., J. G. Field, C. L. Griffiths, and P. Zoutendyk. 1977. The ecology of kelp bed communities in the Benguela upwelling system. Analysis of biomass and spatial distribution. Helgolander wissenschaftliche Meeresuntersuchungen 30:495–518.

Velimirov, B., and C. L. Griffiths. 1979. Wave-induced kelp movement and its importance for community structure. Botanica Marina 22:169–172.

Witman, J. D. 1985. Refuges, biological disturbance, and rocky subtidal community structure in New England. Ecological Monographs 55:421–445.

Wootton, J. T. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. Ecology 75:151–165.