Starfish Predation and the Creation of Mosaic Patterns in a Kelp-Dominated Community

David O. Duggins

Ecology, Vol. 64, No. 6. (Dec., 1983), pp. 1610-1619.

Ecology, 64(6), 1983, pp. 1610–1619

STARFISH PREDATION AND THE CREATION OF MOSAIC PATTERNS IN A KELP-DOMINATED COMMUNITY[1]

David O. Duggins
Friday Harbor Laboratories, Friday Harbor, Washington 98250 USA

Abstract. Subtidal kelps in Torch Bay, Alaska, resemble a mosaic of discrete algal patch types. This pattern reflects the patchy distribution of herbivorous sea urchins (*Strongylocentrotus* spp.) and the rapid successional dynamics of the plant association. Factors potentially causing the aggregated distribution of urchins include physical parameters, food availability, interspecific competition, and starfish predation. Each of these factors is considered, with particular emphasis on predation. The starfish *Pycnopodia helianthoides* is the only predator observed feeding on sea urchins in Torch Bay, and it elicits a strong escape response in two of the three urchin species (and the third at small size). Manipulations of *Pycnopodia* and urchins indicate that predation, by creating even short-lived herbivore-free patches, can significantly affect subtidal algal assemblages, and thus primary productivity, species richness, and species distribution in this important marine community.

Key words: community structure; kelp; predation; Pycnopodia; *sea urchin;* Strongylocentrotus.

INTRODUCTION

The importance of sea urchin grazing as a determinant of nearshore benthic community structure is well established by studies from a wide range of geographical locations (Kitching and Ebling 1961, North 1971, Mann 1977, Vadas 1977). Furthermore, the role of sea urchin predators in ultimately shaping these communities has been demonstrated for northwest Atlantic kelp beds (where the predators are crabs and lobsters; Mann and Breen 1972, Breen and Mann 1976, Bernstein et al. 1981) and for northeast Pacific kelp beds (where the predator is the sea otter, *Enhydra lutris*; Estes and Palmisano 1974, Duggins 1980*a*). While the effects of sea otter predation are predictable, rapid, and dramatic, this urchin predator is rare, with only a few small isolated populations existing over its eastern Pacific range (exclusive of the more numerous populations in the Aleutian Islands). Along the coasts of Oregon, Washington, British Columbia, and southeast Alaska (≈3000 km) there are only three or four such populations, each restricted to areas encompassing <160 km of coastline. The role of other, more common urchin predators along this extensive coastline has been virtually ignored.

Between Oregon and the northern Gulf of Alaska, the abundant starfish *Pycnopodia helianthoides* is the only organism that could be considered an important sea urchin predator (Paine and Vadas 1969, Duggins 1980*b*). The gastropod *Fusitriton oregonensis* (Eaton 1971), wolf eels, and lithoid crabs (D. O. Duggins, *personal observation*) can consume urchins, but the crabs and eels are rare in this benthic community, and *Fusitriton*, while common, eats urchins rarely (D. O. Duggins, *personal observation*). The nature of starfish predation on sea urchins is very different than that of sea otters; *Pycnopodia* coexists with its prey, while otters decimate urchin populations. Thus, while otters affect nearshore kelp beds by removing virtually all important benthic herbivores, the *Pycnopodia* effect is considerably more subtle.

Consumers can clearly be a determinant of community structure by acting to reduce the population size either of key species (e.g., otter-urchin interactions) or of prey species that are competitive dominants (e.g., *Pisaster-Mytilus* interaction; Paine 1966). However, predators could also exert a strong influence on communities by controlling the pattern of prey distribution (in space or time), particularly where such prey distribution alone affects important community parameters. In the example described below, predators create small-scale, prey-free patches by consuming few prey individuals, while the remaining prey exhibit a strong escape response. Since this prey is an herbivore, feeding upon rapidly growing plant species capable of attaining a size refuge, even the short-term creation of prey-free patches can ultimately influence plant diversity and community primary productivity.

In this paper I examine predation by *Pycnopodia* on sea urchins at a study site in southeast Alaska (from which sea otters are absent) with particular consideration given to the relationship between predation and urchin distribution. Though only one locality was studied, most of the organisms under consideration (numerous algal species, three urchin species, and *Pycnopodia*) are found in association throughout the wave-exposed northeast Pacific coast.

METHODS AND RESULTS

In Torch Bay, Alaska (58°20′N, 136°50′W, Fig. 1), the wave-exposed shallow subtidal zone is characterized by a mosaic of algal distribution, which results largely from grazing by three species of sea urchin. Approximately 64% of the substratum is characterized as barren ground (with only encrusting coralline algae

---

[1] Manuscript received 11 September 1981; revised 13 November 1982; accepted 29 November 1982.

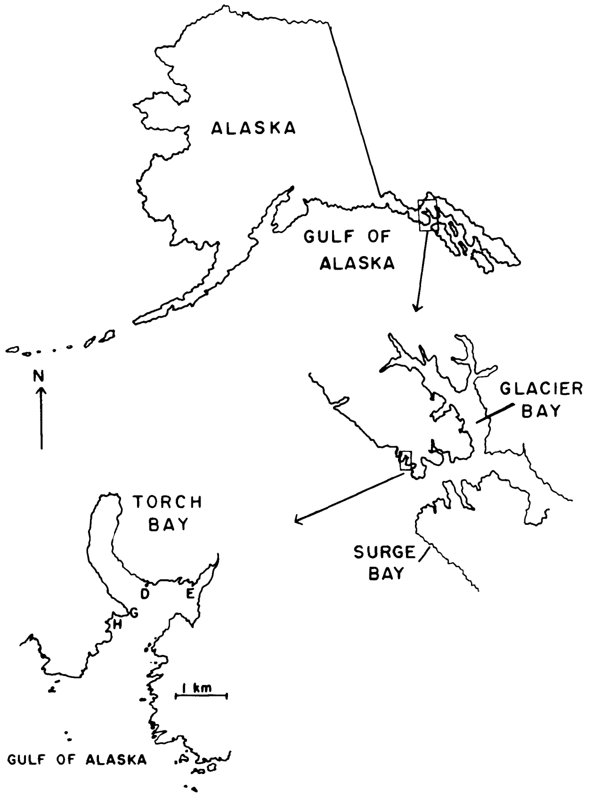

FIG. 1. The study area. Torch Bay is located on the Gulf of Alaska coast in Glacier Bay National Park.

TABLE 1. Variance/mean ratios for three species of urchins at three sites. Data were taken from 0.1-m^2 quadrat counts (N = 200, sites G and H; N = 100, site D) in July 1976. A value of 1.0 would indicate a random distribution within a site.

	Variance/mean ratio		
	Site G	Site D	Site H
S. franciscanus	1.05	1.16	1.13
S. droebachiensis	8.55*	8.78*	3.56*
S. purpuratus	2.09*	5.62*	2.76*

* Significantly different from a random distribution (χ^2, $P < .001$).

present) resulting from urchin overgrazing. About 30% is dominated by annual algal species, which have temporarily escaped urchin grazing. The remaining areas contain the perennial kelp, *Laminaria groenlandica*, in single-species stands, and represent the rarely attained (due to herbivory) endpoint of a rapid algal succession (Duggins 1980*a*). This pattern characterized the community over the 5-yr course of this study. Grazing by urchins (*Strongylocentrotus franciscanus*, *S. droebachiensis*, and *S. purpuratus*) is spatially unpredictable because the pattern of urchin distribution is itself very patchy. Two species (*S. droebachiensis* and *S. purpuratus*) are highly aggregated, while the third assumes a more random distribution (as reflected by variance-to-mean ratios, Fig. 2, Table 1). In shallow water habitats *S. franciscanus* may also be observed in dense aggregations; frequently such aggregations will include both other urchin species as well (Duggins 1981*a*). As will be discussed below, both *S. droebachiensis* and *S. purpuratus* abundances are unpredictable over time at a given site, while *S. franciscanus* densities are relatively constant.

In the summer of 1976 a series of observations and controlled manipulations (using SCUBA) were begun in Torch Bay to investigate urchin distribution pattern and population dynamics. Four factors were considered: (1) physical condition (i.e., depth, substrate type); (2) competition between urchin species; (3) food availability; and (4) predation by *Pycnopodia*.

Physical factors set limits to urchin distribution but contribute little to pattern within those limits. The habitat under consideration (defined as supporting the development of exposed-coast kelp beds) encompasses only a narrow range of physical gradients. Suitable substrata include solid rocky benches or reefs, but not boulder fields or sandy-cobbly substrata. For the most part these benches are physically homogeneous; the microhabitat variations that do occur (e.g., vertical vs. horizontal surfaces, crevices vs. open substrata) do not generate any obvious pattern in urchin distribution. All three species are consistently found on open surfaces with little or no utilization of potential physical refuges from predation or wave surge.

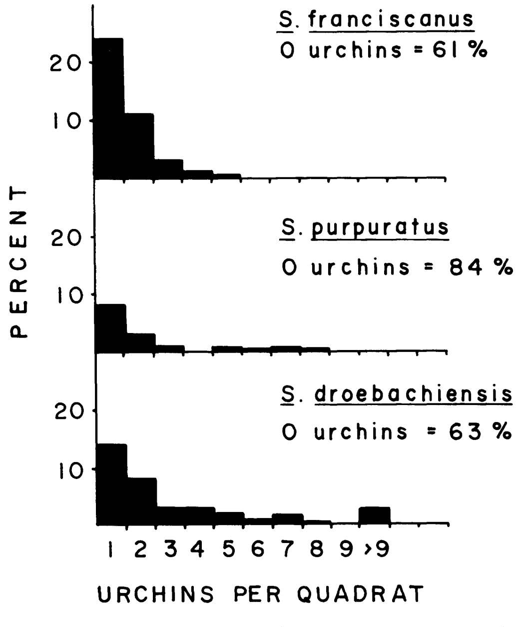

FIG. 2. Frequency distribution of number of urchins in 0.1-m^2 quadrats (N = 500), at three sites. Data are taken from the same sample used in Table 1. Percent of quadrats with 0 urchins is given for each species but is not illustrated.

TABLE 2. Mean gonad indices (gonad wet mass/test diameter) ± SD in urchins taken from well-developed kelp beds (sites G and H) and from areas with no attached macroalgae; $N = 25$. Mean density of kelps (*Nereocystis*, *Alaria*, *Costaria*, *Laminaria*) and *Desmarestia* at site G = 30.8 algae/m^2, at site H = 56.4 algae/m^2. All urchins were collected on the same day, 23 September 1978. There is no significant difference in gonad index between areas for any urchin species (*S. droebachiensis*, $P > .05$; *S. purpuratus* and *S. franciscanus*, $P > .10$, t test).

	Mean gonad index (g/cm)	
	No macroalgae	Kelp bed
S. droebachiensis	2.4 ± 0.5	2.6 ± 0.5 (site G)
S. purpuratus	2.3 ± 0.7	2.0 ± 0.6 (site G)
S. franciscanus	5.3 ± 1.3	5.7 ± 1.4 (site H)

The depth range considered (−3 to −20 m, datum = mean lower low water) is also narrow, but affects urchins in several ways. At depths greater than ≈−20 m, all urchins become rare, probably owing to low food availability. At very shallow depths (<−3 m), urchin numbers and foraging efficiency are reduced due to the effects of wave surge. The only pattern to emerge is that all three species are most dense at depths between −3 and −6 m (discussed below).

I have examined interspecific interactions between the three urchin species elsewhere (Duggins 1981*a*). The conclusions relevant to this analysis are that (1) there is no evidence for negative interactions between species (interference or exploitative competition), and (2) there is strong evidence for a facilitative or positive interaction in some shallow water habitats (≈−3 to −6 m), where high densities of *S. franciscanus* actually attract both *S. droebachiensis* and *S. purpuratus*. The abundance of drift algae in these shallow habitats allows urchin survival at high densities. The facilitative effect is reduced at lower *S. franciscanus* densities and thus is not a factor in most areas.

It is unlikely that the distribution of attached benthic macroalgae significantly influences the distribution of sea urchins. In fact, urchins are only rarely observed to be eating attached adult plants, but subsist primarily by indiscriminate scraping of microalgae and the capture of drift macroalgae. Consequently, the major urchin effect in Torch Bay is not the removal of established kelp beds but the prevention of their development.

Urchins are rarely seen invading stands of annual kelps, in large part because such algae are attractive to urchins only during the short period when they are small (Duggins 1980*b*, 1981*b*). Invasions into stands of the perennial *Laminaria* (which does not achieve a refuge in size) are even rarer, inasmuch as these stands are so uncommon (Duggins 1980*a*). In a similar community, Mattison et al. (1977) pointed out that even within California *Macrocystis* beds, *S. franciscanus* is primarily eating drift algae, and, while urchin movement is greater outside than inside the beds, there is no directional movement by urchins towards higher densities of *Macrocystis*. In Torch Bay, there is no correlation between the density of adult kelps and sea urchins (coefficient of correlation, $r = -0.1$). Furthermore, Table 2 shows there to be no significant difference in gonad index (a measure of food availability) between urchins taken from well-established kelp beds and from long-term barren grounds.

The dependence upon drift algae helps account for the high densities of urchins in shallow water (−3 to −6 m), where attached algae are frequently absent but where drift algae accumulate. Temporary aggregations of urchins around drift algae in deeper water occur, but are uncommon and shortlived (primarily because of discovery and dispersion by *Pycnopodia*). The primary sources of drift algae are the massive annual kelps *Nereocystis leutkeana* and *Alaria fistulosa*, growing in nearby subtidal sites. These kelps have numerous gas-filled chambers (*Alaria*) or a large pneumatocyst (*Nereocystis*) and consequently, when broken free of the substratum, they will usually float on the surface (out of reach of urchins) until washed into shallow water. Most deeper water urchins subsist primarily on what can be scraped from rock surfaces and only occasionally are able to secure a piece of drift (D. O. Duggins, *personal observation*).

The relationship between food availability and urchin distribution cannot, on the basis of my data, be dismissed as unimportant. The patchiness of both microscopic and drift algae could conceivably result in patches of higher urchin density. Of greater interest, however, are factors leading to patches of low urchin density and hence to areas potentially high in algal abundance.

Pycnopodia *predation*

The only significant urchin predator in Torch Bay (in fact the only source of subtidal urchin mortality actually observed in 5 yr of field work) is the starfish *Pycnopodia helianthoides* (Brant) (order Forcipulata). The observed local diet of *Pycnopodia* is given in Fig. 3, which also contrasts the differences between intertidal and subtidal populations. Intertidal *Pycnopodia* are significantly smaller (t test, $P < .001$, Fig. 4) and feed on organisms more easily handled by a small predator. *Pycnopodia* less than ≈25 cm maximum diameter (maximum diameter measured from ray tip to opposite ray tip) rarely feed on urchins (Fig. 4); larger starfish (≥25 cm maximum diameter) are found primarily in the subtidal zone. Small starfish were not observed eating small urchins. Feeding observations for this starfish necessarily reflect the substrate type on which it is found. The more catholic diets observed in Puget Sound (Mauzey et al. 1968) and Prince William Sound (Paul and Feder 1975) probably are indicative of a wider range of habitat types sampled. In

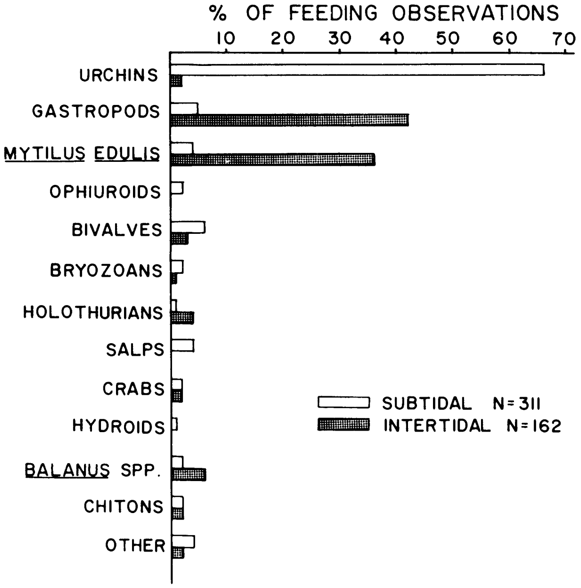

FIG. 3. Intertidal and subtidal feeding observations on *Pycnopodia*. Observations were made over a 5-yr period.

Torch Bay, the low incidence of bivalves in *Pycnopodia*'s diet is a reflection of the fact that most transects were on hard substrates; this is, however, the preferred habitat of *Pycnopodia* here. Both P. K. Dayton (*personal communication*) and I have seen *Pycnopodia* moving from rocky substrates (even when appropriate-sized urchins are nearby) onto soft substrates where they will spend several hours digging out a single buried bivalve. The cause of this seemingly energetically expensive behavior is unknown.

While *Pycnopodia* is the only significant urchin predator in the Torch Bay subtidal, it is very rarely observed feeding on *S. franciscanus*, most of which have reached a size refuge. Fig. 5 shows the size distribution of urchins in *Pycnopodia*'s diet compared to those available. This analysis is not broken down by urchin species because digestion is usually internal (unlike many other starfish) and prey species identification is impossible without harming the starfish. It is, however, possible to get approximate test diameter measurements (±1 cm) of ingested urchins by feeling directly through the body wall of this soft-bodied starfish. *Pycnopodia* prefers urchins in the 6–8 cm test diameter (t.d.) size classes, and this virtually eliminates *S. franciscanus* from its diet. *S. franciscanus* <9 cm t.d. are rare in Torch Bay populations. In fact, small individuals (<5 cm t.d.) were observed only in 1979 and then in such low numbers that they did not occur in random samples for size distributions. Only five observations in 5 yr (over 2500 person-hours of diving) were made of *Pycnopodia* feeding (external digestion) on *S. franciscanus*, and these were primarily on individuals at the small end of the available size spectrum (t.d. = 7, 8, 9, 9, 12 cm). *S. franciscanus* even loses its escape response from *Pycnopodia* as it reaches its size refuge. This was demonstrated in an experiment in which *S. franciscanus* of various sizes were stimulated by touching their tests with a *Pycnopodia* ray for 30 s. Fig. 6 shows the distance moved, as a function of urchin size, over the following 3 min.

Pycnopodia predation upon small *S. franciscanus* may be more important in those rare years when recruitment occurs, as well as in the following years, until a cohort reaches the size refuge. Very small individuals have been observed underneath the tests and among the spines of adults (Tegner and Dayton 1977); such a habitat would be an effective refuge from *Pycnopodia* predation. Although factors regulating *S. franciscanus* populations in Torch Bay are unknown, some adults were observed to be suffering from a disease that erodes their spines. Mass mortalities of *S. franciscanus* from disease have been noted in California populations (Pearse et al. 1977).

The 6–8 cm test diameter size classes which are seemingly preferred by *Pycnopodia* (Fig. 5) correspond both to the maximum sizes obtained by *S. droebachiensis* and *S. purpuratus* and to the most common size classes observed in their Torch Bay populations (Fig. 5). Thus neither of these species is capable of reaching a size refuge. Both species are commonly eaten by *Pycnopodia*, but species-specific sample sizes are too small (and urchin species composition at a given location too variable) to construct electivities or comment on preference for one species over the other.

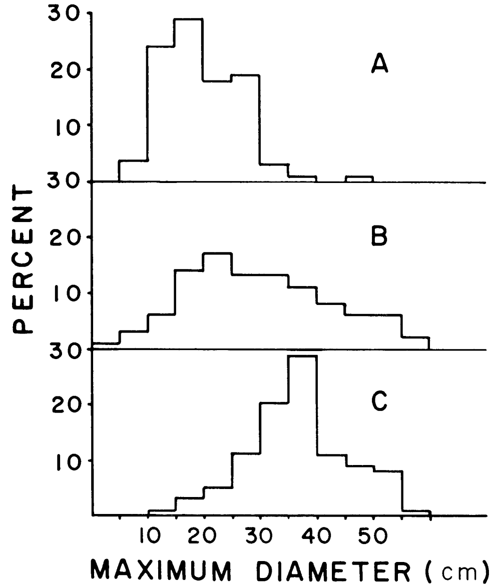

FIG. 4. Size frequency distributions for *Pycnopodia* in the intertidal (A, $N = 89$) and subtidal (B, $N = 574$) zones. C gives the size frequency distribution of subtidal *Pycnopodia* observed to be eating sea urchins ($N = 99$).

Fig. 5 also illustrates the most significant ecological difference between *S. droebachiensis* and *S. purpuratus* in Torch Bay. In >5 yr (1975–1979) I never encountered a *S. purpuratus* <4 cm t.d.. It appears that *S. purpuratus* recruitment in southeast Alaska is infrequent, as it is along the coast of Washington and Oregon (Gonor 1973, R. T. Paine, *personal communication*). *S. droebachiensis*, however, recruits successfully each year; small (<2 cm t.d.) individuals could always be found among cobbles and boulders in the low intertidal zone and in mixed species aggregations in the shallow subtidal zone.

The rate of *Pycnopodia* predation on sea urchins can be estimated using methods described by Birkeland (1974). Laboratory experiments indicate that ≈28 h (mean ± SD = 28.0 + 5.9, $N = 11$) are required to capture, consume, and egest an urchin in the preferred size range (6–8 cm t.d.). In the field, 19% of all *Pycnopodia* observed were feeding on urchins ($N = 1154$ total observations, of which 824 were not feeding). Birkeland's formula for feeding rates is ZW/Y, where Z = proportion of *Pycnopodia* seen feeding on urchins multiplied by proportion of urchins in *Pycnopodia*'s diet; W = proportion of successful attacks on urchins; and Y = duration of attack. Here $W = 1.0$, since once an attack has begun, *Pycnopodia* always seems to be successful. With $Z = 0.19 \times 0.68$ and $Y = 1.1$ d, I calculate that 0.12 urchin is eaten per *Pycnopodia* per day, or 44 urchins per *Pycnopodia* per year. Twenty-four randomly placed transects censused for *Pycnopodia* density (in the size range likely to be eating urchins, >25 cm total diameter, see Fig. 4) generated a mean of 1.8 ± 1.1 *Pycnopodia*/20 m^2. Evaluation of the overall effect of *Pycnopodia* predation on urchin population density must be made with considerable caution, due to the high standard deviations in all urchin density estimates. Maximum densities reach >200 urchins/m^2 for both *S. purpuratus* and *S. droebachiensis*; however, the occurrence of areas with both of these species absent (or present in very low densities) results in mean densities with intractably high variances (mean ± SD: *S. droebachiensis* = 6 ± 14, *S. purpuratus* = 4 ± 13; see Duggins 1980*a* for methods). However, given the above predation rates, *Pycnopodia* is likely to be an important factor in the regulation of local urchin populations, particularly with regard to *S. purpuratus* (with its rare and unpredictable recruitment).

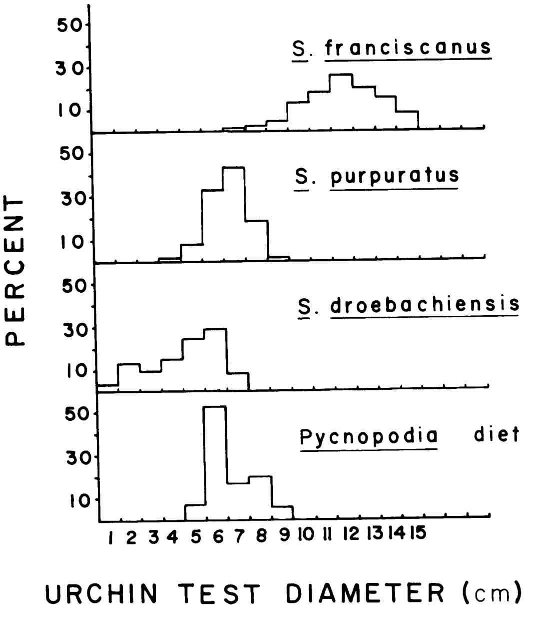

FIG. 5. Size frequency distributions for three species of urchins in Torch Bay (*S. franciscanus*: $N = 485$; *S. purpuratus*: $N = 455$; *S. droebachiensis*: $N = 351$) and for all urchins in the diet of *Pycnopodia* ($N = 49$). Data were pooled from measurements taken over 5 yr.

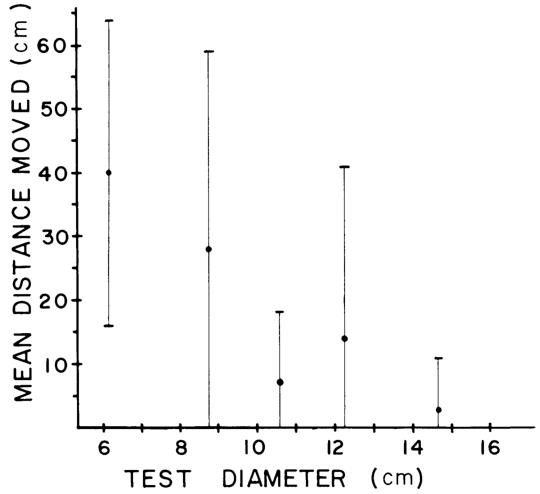

FIG. 6. Relationships between distance moved by *S. franciscanus* (when stimulated by *Pycnopodia*) and urchin maximum test diameter. Correlation coefficient = −0.51, $N = 49$, probability of independence, $P < .001$. Bars represent one standard deviation.

Urchin escape response

While the experimental removal of *Pycnopodia* would probably lead to a gradual increase in the population sizes of the three urchin species, this was not practical because of the very slow recruitment of *S. purpuratus* and *S. franciscanus*. An examination of the behavioral interactions between predator and prey, however, provided considerable insight into community structure on a local scale. I have shown elsewhere (Duggins 1981*a*) that the addition of a single *Pycnopodia* to a large, mixed-species urchin aggregation leads to the rapid disappearance (through escape rather than consumption) of *S. droebachiensis* and *S. purpuratus*. Fig. 6 shows that small *S. franciscanus* also exhibit a strong escape response. To assess the starfish-urchin

TABLE 3. Mean densities (± standard deviation) of key organisms in the *Pycnopodia* addition area and control. Densities are number per 0.1 m^2 (urchins and kelps) and number per 20 m^2 (*Pycnopodia*). Addition area was roughly 400 m^2, control area 200 m^2. *S.f.* = *Strongylocentrotus franciscanus*; *S.p.* = *S. purpuratus*; *S.d.* = *S. droebachiensis*; *N* = *Nereocystis luetkeana*; *A* = *Alaria fistulosa*; *C* = *Costaria costata*; *L* = *Laminaria groenlandica*; *Pyc* = *Pycnopodia helianthoides*. ND = data not taken.

Treatment	Species	July 1976*	September 1976†	March 1977	May 1977	20 August 1977	22 August 1977‡	3 September 1977
Addition					Population density ± SD			
	Pyc	0.3 ± 0.5	6.4 ± 5.6	3.1 ± 2.3	3.0 ± 3.2	1.3 ± 1.1	5.6 ± 4.9	3.7 ± 2.4
Urchins	*S.f.*	0.7 ± 0.9	0.6 ± 0.8	0.6 ± 1.0	0.9 ± 1.1	0.6 ± 0.8	0.6 ± 0.8	0.7 ± 1.0
	S.p.	0.3 ± 0.9	0.4 ± 1.4	0.2 ± 1.1	0	0	0	0.1 ± 0.2
	S.d.	1.6 ± 2.4	0.5 ± 1.6	0.3 ± 0.9	0.1 ± 0.3	0.9 ± 3.1	0.4 ± 1.5	0.2 ± 1.1
Kelps	*N*	0.01 ± 0.07	ND	ND	1.23 ± 2.95	ND	ND	ND
	A	0.04 ± 0.32	ND	ND	1.07 ± 2.60	ND	ND	ND
	C	0.07 ± 0.48	ND	ND	0.51 ± 1.40	ND	ND	ND
	L	0.06 ± 0.59	ND	ND	0.44 ± 1.29	ND	ND	ND
Control								
	Pyc	2.8 ± 2.6	1.4 ± 1.1	0.8 ± 1.3	1.8 ± 1.3	ND	ND	6.4 ± 1.5
Urchins	*S.f.*	1.3 ± 1.1	0.9 ± 0.8	1.0 ± 0.9	0.9 ± 0.8	ND	ND	0.8 ± 0.8
	S.p.	0.3 ± 1.3	0.2 ± 1.1	0.4 ± 1.5	0.4 ± 2.1	ND	ND	0.1 ± 0.7
	S.d.	0.6 ± 2.4	0.4 ± 1.0	0.3 ± 0.8	0.4 ± 1.3	ND	ND	0
Kelps	*N*	0	ND	ND	0.05 ± 0.33	ND	ND	ND
	A	0.18 ± 0.93	ND	ND	0.32 ± 1.16	ND	ND	ND
	C	0	ND	ND	0.15 ± 0.76	ND	ND	ND
	L	0	ND	ND	0.16 ± 0.73	ND	ND	ND

* Before *Pycnopodia* addition.
† Following first *Pycnopodia* addition.
‡ Following second *Pycnopodia* addition.

relationship further, two types of experiments were performed. In the first, *Pycnopodia* densities were manipulated over a large area to determine the effect on urchins (and consequently on kelp). In the second, urchin densities were increased to evaluate the response of *Pycnopodia* to urchin aggregation.

Beginning in late July 1976, *Pycnopodia* were added to an isolated subtidal reef that initially had few starfish, high densities of all three urchin species, and very few kelps. Ten parallel transect lines (10 m long) were laid out across the reef and their positions permanently marked. Twenty quadrats were censused on each line (total of 200 quadrats). A second, smaller reef (5 transects, N = 100 quadrats) served as a control. The control site was similar in depth, exposure, and substrate to the experimental site. It was impossible to find a control with exactly the same beginning densities of all key organisms. Initially (July 1976) the control had higher *Pycnopodia* and *S. franciscanus* densities and lower *S. droebachiensis* densities (t tests, $P < .01$: all t tests and ANOVAs below were performed on (log + 1)-transformed data). However, if one compares the mean number of all urchins (pooling the three species), the two areas show no significant differences (t test, $P > .2$). Considering urchins in such a pooled manner is reasonable when looking at urchin-kelp interactions, given the similarity of the three species' diets and hence their effects on algal associations (Duggins 1981*a*). In July 1976, the control area and the experimental area both had very low kelp densities (Table 3). Short-term urchin removals performed at the control site in the previous year (Duggins and Quinn 1977) indicated that in the absence of urchins, kelps are capable of flourishing there as well.

Following the addition of *Pycnopodia*, *S. droebachiensis* was observed to move rapidly off the reef into deeper water. *S. purpuratus* densities dropped more slowly, but by May 1977 this species had entirely disappeared from the experimental reef. While some small urchins were consumed by the starfish, the lowered densities in early September 1976 (Table 3) were primarily the result of a behavioral escape response. Heavy *Pycnopodia* predation would have resulted in the accumulation of large numbers of empty urchin tests at the site; the few such tests observed were only a small fraction of the number of urchins that disappeared.

The results of this experiment are given in Table 3 (initiated July 1976, terminated May 1977). *S. franciscanus* densities were unaffected by the addition of *Pycnopodia*, while by May 1977 *S. purpuratus* and *S. droebachiensis* densities fell to 0.1 and 0/0.1 m^2, respectively. Densities of both small species of urchin remained relatively constant in the control during the period July 1976 to May 1977 (ANOVA on *S. droebachiensis*, $P > .1$, on *S. purpuratus*, $P > .1$). The

TABLE 4. Urchin addition experiment. *Pycnopodia* and empty test counts are total number observed within a 5 m radius of the center of the addition site. There were no urchins in the control area. Urchin additions were performed on 25 August 1977. N.A. means no sample taken.

	Urchin density (no./0.1 m², $\bar{x}$ ± SD)			
	24 August	26 August	10 September	22 October
		S. droebachiensis addition		
S. droebachiensis	0	4.4 ± 2.8	0	0
Pycnopodia	0	0	5	1
Empty tests	0	N.A.	N.A.	2
		S. purpuratus addition		
S. purpuratus	0	6.0 ± 3.7	4.4 ± 4.8	0
Pycnopodia	0	0	7	14
Empty tests	0	N.A.	N.A.	50
		S. franciscanus addition		
S. franciscanus	0	0.9 ± 0.8	0.8 ± 1.0	0.7 ± 0.9
Pycnopodia	0	0	0	0
Empty tests	0	N.A.	N.A.	0
		Control		
Pycnopodia	0	0	0	0
Empty tests	0	N.A.	N.A.	0

decline in *S. droebachiensis* in the addition area becomes even more apparent when one considers that its beginning densities were more than twice as great in this area as in the control (Table 3).

Two further events at these sites support the hypothesis that *Pycnopodia* is important in determining local urchin density. By 20 August 1977, *Pycnopodia* density had fallen considerably in the addition area. This decrease was accompanied by a rise in *S. droebachiensis* densities (May 1977 vs. 20 August 1977) as urchins from deeper water moved back onto the reef (D. O. Duggins, *personal observation*). On 21 August 1977 I re-added *Pycnopodia* to the addition area, and 24 h later (22 August 1977) recensused the site (Table 3). Even in this short time, the increased starfish density resulted in a significant reduction in *S. droebachiensis* (t test on *S. droebachiensis* 22 vs. 20 August, $P < .01$). By 3 September 1977, small urchins were again at very low densities in the addition area. Time did not allow censuses of the control site on 20 or 22 August 1977.

Parallel natural events occurred in the control area in September 1977 (Table 3), where *Pycnopodia* invaded to densities comparable to those in the manipulation. There was a concurrent decrease in *S. purpuratus* and *S. droebachiensis* densities (t test, May 1977 vs. September 1977, *S. droebachiensis* and *S. purpuratus* pooled, $P < .01$), verifying the predictions generated by the experiment. As in the starfish addition, urchins in this control area apparently fled in response to increased *Pycnopodia* densities; few of the invading starfish were observed to be eating urchins, and few empty tests accumulated.

A second set of experiments leads to similar conclusions regarding *Pycnopodia*-urchin interactions. Four intertidal reefs (similar depth, substrate, and exposure) were found which contained similar stands of the kelps *Nereocystis* and *Alaria*. None of these stands originally had any urchins associated with it. To each of three stands I added one species of urchin to high density (but well below normally occurring maximum density); one stand received only *S. droebachiensis*, one received only *S. purpuratus*, etc. The fourth stand received no urchins. I removed all *Pycnopodia* from within 20 m of each stand (few were present). Urchin and starfish densities and accumulated empty tests over the following 58 d at the four sites are given in Table 4. Urchins were added on 25 August 1977, and the areas were censused after 1, 16, and 58 d. At each census I counted *Pycnopodia* within a 5 m radius of the experiment's center. By the 10 September 1977 census, both the *S. droebachiensis* and *S. purpuratus* additions had attracted large numbers of starfish. Urchin density in the *S. droebachiensis* area dropped to 0, and by 22 October the *S. purpuratus* addition also contained no urchins. The *S. franciscanus* addition attracted no starfish and experienced only a small drop in urchin density. The control area (containing no urchins) experienced no invasion of *Pycnopodia*. The accumulation of empty tests in the *S. purpuratus* area (Table 4) indicates some consumption by *Pycnopodia*. However, given that several hundred urchins were present in each area on 26 August, the small number of tests again indicates that most urchins moved out of the area. I observed this movement during the course of several dives between 26 August and 10 September. I have described elsewhere (Duggins 1981*a*) manipulations in which mixed urchin species aggregations were created, some containing *S. droebachiensis* and *S. purpuratus*, and some with all three urchin species. In all instances, aggregations containing only the small urchin species were rapidly discovered and dispersed by *Pycnopodia*. All the above experiments demonstrate that both artificial and natural increases in *Pycnopodia* density can have rapid and dramatic effects on local urchin densities.

The algal response

A linkage between the above predator-prey behavioral interactions and benthic algal productivity could be a key element in the structure of this nearshore benthic community. The relationship between the urchin-starfish "cat and mouse game" and algal abundance can be evaluated on the basis of the above experiments and previously reported studies. It is clear that in Torch Bay, the experimental removal of all urchins leads to the development of diverse and highly productive stands of benthic algae (Duggins 1980*a*).

In the *Pycnopodia* addition experiment (Table 3), dramatic differences in emergent kelp associations between the addition and control sites (May 1977) resulted from subtle differences in overall mean urchin density. In May 1977 there was no difference in the density of *S. franciscanus* between the two sites, but the total density of small urchins (*S. purpuratus* plus *S. droebachiensis*) was much greater in the control (0.8 urchins/0.1 m^2) than in the starfish addition (0.1 urchins/0.1 m^2). When all three urchin species are considered together, there were significantly higher densities in the control on both the March 1977 sampling date (*t* test, $P < .01$) and the May 1977 sampling date ($P < .001$). These differences developed in spite of the fact that total urchin density was greater in the addition area at the beginning of the experiment.

The macroscopic sporophyte stages of these kelps are just beginning to develop in late March, and they are most vulnerable to urchin grazing when small (large *Alaria* and *Nereocystis* are unattractive to urchins; Duggins 1980*b*, 1981*b*). While some gametophytes probably were removed previous to March by indiscriminate urchin scraping, it is the period between March and early June when urchins are observed feeding on small kelps (D. O. Duggins, *personal observation*). Table 3 gives mean densities for the four most common subtidal kelps in Torch Bay at the beginning of the experiment (July 1976: little difference between addition area and control; *t* test, all kelps pooled, $P >$ .5), and in May 1977. The May census showed a flourishing kelp bed at the *Pycnopodia* addition site, with densities much higher than in the control (*t* test, all kelps pooled, $P < .001$). Furthermore, this bed developed in a year when kelp density declined at other sites (Duggins 1981*b*). It seems highly likely that this algal development resulted from a springtime decline in urchin numbers (actually a decline in *S. purpuratus* and *S. droebachiensis*) that was ultimately caused by the *Pycnopodia* manipulation.

The dispersal of urchins by *Pycnopodia* may be only a temporary event (*Pycnopodia* did move out of the addition area and *S. droebachiensis* reinvaded), but the rapid growth of kelps and the existence of a size refuge from urchin grazing for several important species guarantees that even short-term release from herbivory results in the survival of many benthic algae.

DISCUSSION

Most ecological communities consist of patchworks or mosaics of a variety of species rather than homogeneous assemblages evenly distributed in space. Disturbance-induced mosaic patterns are now well documented as an integral characteristic of a wide range of community types, including temperate and tropical forests, prairies, and intertidal and subtidal rocky and soft-sediment marine areas (see VanBlaricom 1982, Dethier 1984 for relevant references). Patchy arrays of species have important ramifications to community structure by imparting heterogeneity which ultimately affects ecological processes. The importance of heterogeneity, both physical and biological, has long been recognized (Mac Arthur and Mac Arthur 1961, Smith 1972) and recent innovations in modelling the relationships between spatio-temporal heterogeneity and ecological structure (Levin and Paine 1974, Caswell 1978, Paine and Levin 1981, Runkle 1982) provide a useful alternative to viewing communities as equilibrium states.

Small-scale disturbance events are a source of such heterogeneity in that they create patches within the community that differ from one another in species composition, ecological process, or population age structure. Species composition can vary between patches when the unpredictable order of recruitment following disturbance results in assemblages determined by priority effects (e.g., Sutherland and Karlson 1977). Ecological processes may differ between patches when, for instance, (1) the intensity or even the direction of competition varies from place to place within a single community (Connell 1975, Jackson and Buss 1975), or (2) predator foraging varies in rate and selection between patches (Mac Arthur 1972, Schoener 1974, Cowie and Krebs 1979). The ability of some organisms to reach a size refuge from certain types of disturbance may lead to the creation of a patch that differs from the surrounding "landscape" in that it contains individuals of greater size/age and probably reproductive output. Such a refuge may simply be the result of reaching a large size, as in *S. franciscanus* (this study) or in mussels (Paine 1976), or of larger/older individuals generating some effective defense mechanism (chemical or structural) that is absent in younger individuals. While size may be an effective defense against consumer-generated disturbance, large individuals may actually be more vulnerable to physical disturbances such as blowdowns in forests or wave battering in intertidal mussel beds. If consumer-induced disturbance is an important community feature, and if the expression of such disturbance is itself patchy (i.e., the consumers are distributed in a patchy manner), then a given area may, simply by chance, avoid detection until prey individuals reach a safe size.

In the shallow subtidal communities considered in this paper, algal pattern is characterized by discrete patch types. High urchin density produces and maintains patches of barren substratum, while areas free from urchin grazing are rapidly colonized by fast-growing, highly productive kelps. Susceptibility of these patches to further urchin grazing is a function of patch age; older stands of annuals are much less vulnerable. Were there no such size refuge, annual kelps would probably never survive long enough to attain full adult size (and maximum productivity). The rapid displacement of annual species (*Nereocystis, Alaria, Costaria*) by a competitively dominant perennial species (*Laminaria*) with no such size refuge guarantees that eventually the patch will again be grazed to a barren state and hence heterogeneity will be maintained (Duggins 1980*a*).

The key to this pattern is the patchy nature of urchin distribution. Were urchin biomass distributed uniformly or even randomly, no single space would be likely to escape urchin grazing long enough for the pattern to develop. Areas of high urchin density may result from two factors: an ephemeral source of food, particularly concentrations of drift algae; or the formation and persistence of large three-species aggregations which serve as refuges from starfish predation (for *S. droebachiensis* and *S. purpuratus*, Duggins 1981*a*). While random movement of urchins must also be recognized as a factor in urchin distribution, areas of low urchin density result in large part from the behavioral interaction of sea urchins and their starfish predator. Both experimental manipulation of *Pycnopodia* and observation of natural populations indicate that large areas can be cleared of small urchins by *Pycnopodia* (when *S. franciscanus* are not superabundant) and remain cleared long enough for kelp to become established. This clearing action is not accomplished by consumption of all available small urchins as much as it is by these mobile prey rapidly vacating areas invaded by *Pycnopodia*.

The nature of this starfish-urchin interaction suggests a somewhat different way of interpreting the role of predators in structuring communities. Predators can clearly reduce prey populations through actual consumption, but in this instance they seem to be having a more significant effect by simply moving their prey around in space. While this applies to only two of the three urchin species (and the third at small size), these two species account for >63% of the total urchin population in Torch Bay (Duggins 1980*a*). Where starfish-mediated reductions of *S. purpuratus* and *S. droebachiensis* populations coincide with areas of low *S. franciscanus* density, the potential for rapid kelp development exists. Similarly, Garrity and Levings (1981) have demonstrated that in a tropical rocky intertidal community, concentrations of predatory gastropods are avoided by herbivorous gastropods; the resultant herbivore-free patches are significantly different (with respect to primary space occupiers) from patches where the predators are absent.

In Torch Bay, as in other nearshore marine systems, urchins set limits to the distribution, abundance, and ultimately productivity of benthic algae. The importance of this productivity results from its direct utilization, indirect utilization through detritus-based food webs, and from the use of kelp beds as refuges from predation by nearshore pelagic organisms. *Pycnopodia* is the only widespread predator on sea urchins along the northeast Pacific coastline. Unlike the rare sea otter which decimates urchin populations and establishes an alternative steady state, this starfish predator appears to exist in a dynamic equilibrium with its preferred prey. This large-scale equilibrium is contrasted with events at a local scale (measured in tens or hundreds of square metres) which are considerably more variable. Such localized predator-prey interactions may ultimately be responsible for the observed mosaic pattern of benthic algae.

ACKNOWLEDGMENTS

I would like to thank the many people who assisted me in the field, especially Gregory P. Streveler, then research biologist at Glacier Bay National Monument. The manuscript greatly benefitted from criticisms by Megan Dethier, Sarah Woodin, R. T. Paine, P. K. Dayton, and an anonymous reviewer. Research was conducted under grants from the National Park Service (CX 9000-6-0135).

LITERATURE CITED

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

Birkeland, C. 1974. Interactions between a sea pen and seven of its predators. Ecological Monographs **44**:211–232.

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.

Caswell, H. 1978. Predator-mediated coexistence: a nonequilibrium model. American Naturalist **112**:127–154.

Connell, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pages 460–490 *in* M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts, USA.

Cowie, R. J., and J. R. Krebs. 1979. Optimal foraging in a patchy environment. Symposia of the British Ecological Society **20**:183–205.

Dethier, M. N. 1984, *in press*. Disturbance and recovery in intertidal pools: maintenance of mosaic patterns. Ecological Monographs.

Duggins, D. O. 1980*a*. Kelp beds and sea otters: an experimental approach. Ecology **61**:447–453.

———. 1980*b*. Kelp dominated communities: experimental studies on the relationships between sea urchins, their predators and their algal resources. Dissertation. University of Washington, Seattle, Washington, USA.

———. 1981*a*. Interspecific facilitation within a guild of benthic marine herbivores and its effect on community structure. Oecologia (Berlin) **48**:157–163.

———. 1981*b*. Sea urchins and kelp: the effects of short term changes in urchin diet. Limnology and Oceanography **26**:391–394.

Duggins, D. O., and J. F. Quinn. 1977. Keystone predators and marine community structure. Pages 95–106 *in* G. P. Streveler and I. A. Worley, editors. Dixon Harbor biological survey. National Park Service, Juneau, Alaska, USA.

Eaton, C. M. 1971. The reproductive and feeding biology of the prosobranch gastropod *Fusitriton oregonensis* (Redfield) (Fam. Cymatiidae). Thesis. University of Washington, Seattle, Washington, USA.

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

Garrity, S. D., and S. C. Levings. 1981. A predator-prey interaction between two physically and biologically constrained tropical rocky shore gastropods: direct, indirect and community effects. Ecological Monographs **51**:267–286.

Gonor, J. F. 1973. Reproductive cycles in Oregon populations of the echinoid *Strongylocentrotus purpuratus* (Stimpson). I. Annual gonad growth and ovarian gametogenic cycles. Journal of Experimental Marine Biology and Ecology **12**:45–64.

Jackson, J. B. C., and L. Buss. 1975. Alleopathy and spatial competition among coral reef invertebrates. Proceedings of the National Academy of Sciences (USA) **72**:5160–5163.

Kitching, J. A., and F. J. Ebling. 1961. The ecology of Lough Ine. II. The control of algae by *Paracentrotus lividus* (Echinoidea). Journal of Animal Ecology **30**:373–384.

Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation and community structure. Proceedings of the National Academy of Sciences (USA) **71**:2744–2747.

Mac Arthur, R. H. 1972. Geographical ecology: patterns in the distribution of species. Harper and Row, New York, New York, USA.

Mac Arthur, R. H., and J. Mac Arthur. 1961. On bird species diversity. Ecology **42**:594–598.

Mann, K. H. 1977. Destruction of kelp beds by sea urchins: a cyclical phenomenon or irreversible degradation? Helgolander wissenschaftliche Meeresuntersuchungen **30**:455–467.

Mann, K. H., and P. A. Breen. 1972. The relationship between lobster abundance, sea urchins and kelp beds. Journal of the Fisheries Research Board of Canada **29**:603–605.

Mattison, J. E., J. D. Trent, A. L. Shanks, T. B. Akin, and J. S. Pearse. 1977. Movement and feeding activity of red sea urchins (*Strongylocentrotus franciscanus*) adjacent to a kelp forest. Marine Biology **39**:25–30.

Mauzey, K. P., C. Birkeland, and P. K. Dayton. 1968. Feeding behavior of asteroids and escape responses of their prey in the Puget Sound region. Ecology **49**:603–619.

North, W. J., editor. 1971. The biology of giant kelp beds (*Macrocystis*) in California. Nova Hedwigia **32**:1–600.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist **100**:65–75.

———. 1976. Size-limited predation: an observational and experimental approach with the *Pisaster-Mytilus* interaction. Ecology **57**:858–873.

Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs **51**:145–178.

Paine, R. T., and R. L. Vadas. 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. Limnology and Oceanography **14**:710–719.

Paul, A. J., and H. M. Feder. 1975. The food of the sea star *Pycnopodia helianthoides* (Brant) in Prince William Sound, Alaska. Ophelia **14**:15–22.

Pearse, J. S., D. P. Costa, M. B. Yellin, and C. R. Agegian. 1977. Localized mass mortality of red sea urchins, *Strongylocentrotus franciscanus*, near Santa Cruz, California. Fisheries Bulletin **75**:645–648.

Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology **63**:1533–1546.

Schoener, T. A. 1974. The compression hypothesis and temporal resource partitioning. Proceedings of the National Academy of Sciences (USA) **71**:4169–4172.

Smith, F. E. 1972. Spatial heterogeneity, stability and diversity in ecosystems. Transactions of the Connecticut Academy of Arts and Sciences **44**:307–336.

Sutherland, J. P., and R. H. Karlson. 1977. Development and stability of the fouling community at Beaufort, North Carolina. Ecological Monographs **47**:425–446.

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

Vadas, R. L. 1977. Preferential feeding: an optimization strategy in sea urchins. Ecological Monographs **47**:337–371.

VanBlaricom, G. R. 1982. Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell. Ecological Monographs **52**:283–305.