

THE KEYSTONE SPECIES CONCEPT: VARIATION IN INTERACTION STRENGTH IN A ROCKY INTERTIDAL HABITAT¹

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We dedicate this paper to the memory of John P. Sutherland, a great scientist, a great human being.

Abstract. The usefulness and generality of the keystone species concept has recently been questioned. We investigated variation in interaction strength between the original keystone predator, the seastar *Pisaster ochraceus*, and its primary prey, mussels (*Mytilus californianus* and *M. trossulus*). The study was prompted by differences in community structure at two low zone sites along the central Oregon coast, Boiler Bay (BB) and Strawberry Hill (SH). Predators, especially seastars, were larger and more abundant at SH than at BB. Further, sessile animals were more abundant and macrophytes were less abundant at SH. Predators were more abundant at wave-exposed sites at both sites, and at SH, sessile invertebrates were more abundant at the wave-exposed location and sand cover was high at the wave-protected location. To test the hypothesis that variation in predation strength explained some of these differences, we examined the seastar–mussel interaction at locations with high and low wave exposure at both sites. Predation intensity was quantified by determining the survival of mussels in clumps (50 mussels per clump, shell length 4–7 cm) transplanted to large plots (18–163 m²) with or without seastars in the low intertidal zone. Predation effects were quantified by determining prey recolonization rates in marked quadrats in the same large plots. Spatial variation in interaction strength was quantified by examining predation at scales of metres (among transplants within plots), 10's of metres (between replicate plots within each exposure at each site), 100's of metres (between wave exposures within locations), and 10 000's of metres (between sites). Temporal variation was evaluated by performing the experiments in 1990 and 1991. The relation between prey (mussel) recruitment and growth to differences in community structure was evaluated by quantifying recruitment density in plastic mesh balls (collectors) and growth of individually marked transplanted mussels, respectively, at each site × exposure × tide level combination each month for 4 yr.

Predation intensity varied greatly at all spatial scales. At the two largest spatial scales (10's of kilometres, 100's of metres), differences in both survival of transplanted mussels and prey recolonization depended on variation in seastar abundance with site, wave exposure, prey recruitment and growth, and at SH protected, the extent of sand burial. Variation at the two smallest scales (metres, 10's of metres) was high when seastars were scarce and low when seastars were abundant. Transplanted mussels suffered 100% mortality in 2 wk at wave-exposed SH, but took > 52 wk at wave-protected BB. Seastar effects on prey recolonization were detected only at the SH wave-exposed site. Here, where prey recruitment and growth were unusually high, the mussel *M. trossulus* invaded and dominated space within 9 mo. After 14 mo, whelks, which increased in both size and abundance in the absence of *Pisaster*, arrested this increase in mussel abundance. Similar changes did not occur at other site × exposure combinations, evidently because prey recruitment was low and possibly also due to whelk predation on juveniles. Longer term results indicate that, as in Washington state, seastars prevent large adult *M. californianus* from invading lower intertidal regions, but only at wave-exposed, not wave-protected sites. Thus, three distinct predation regimes were observed: (1) strong keystone predation by seastars at wave-exposed headlands; (2) less-strong diffuse predation by seastars, whelks, and possibly other predators at a wave-protected cove, and (3) weak predation at a wave-protected site buried regularly by sand.

Comparable experimental results at four wave-exposed headlands (our two in Oregon and two others in Washington), and similarities between these and communities on other West Coast headlands suggest keystone predation occurs broadly in this system. Results in wave-protected habitats, however, suggest it is not universal. In Oregon, keystone predation was evidently contingent on conditions of high prey production (i.e., recruitment and growth), while diffuse predation occurred when prey production was low, and weak predation occurred when environmental stress was high. Combining our results with examples from other marine and non-marine habitats suggests a need to consider a broader range of models than just keystone predation. The predictive and explanatory value of an expanded set of models depends on identifying factors distinguishing them. Although evidence is limited, a survey of 17 examples suggests (1) keystone predation is evidently not distinguished from diffuse predation by any of 11 previously proposed differences, but (2) may be distinguished by rates of prey production. Further, (3) differential predation on competitively dominant prey does not distinguish keystone from nonkeystone systems, since this interaction occurs in both types of community. Instead, differential predation on dominant prey evidently distinguishes strong-from weak-predation communities. While the keystone predation concept has been and will continue to be useful, a broadened focus on testing and developing more general models of community regulation is needed.

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INTRODUCTION

Since it was first introduced by Paine (1969), the keystone species concept has been a central organizing principle in community ecology (Mills et al. 1993). Recently, however, both the usefulness and generality of this concept have been questioned (Strong 1992, Mills et al. 1993). Some criticism derives from ambiguities in definition, leading to either very broad or very narrow usage. For instance, the term "keystone," although originally applied to a top carnivore, has been used broadly to refer to important but noncarnivorous species (e.g., herbivores, prey, mutualists, hosts, or species modifying habitats through nontrophic interactions; National Research Council 1986, Bond 1993, Mills et al. 1993). In contrast, Strong (1992:747), in his stimulating critique of the trophic cascade concept, states "true trophic cascades imply keystone species . . . , taxa with such top-down dominance that their removal causes precipitous change in the system." He later constrains "precipitous change" to mean either near-elimination of autotrophs (three-level systems) or rapid increase to high abundance of autotrophs (four-level systems). This usage seems unnecessarily restricted, however, as it implicitly excludes other changes resulting from the activities of keystone species, such as those in species composition or size (e.g., Paine 1966, 1974, Carpenter et al. 1987).

Definitions

Here we consider just one type of keystone species, keystone predators. To avoid ambiguity, a "keystone predator" is defined as only one of several predators in a community that alone determines most patterns of prey community structure, including distribution, abundance, composition, size, and diversity. Thus, a predator is not a keystone if: (1) total predation is moderate to strong but each of the predators alone has little measurable effect (here termed "diffuse" predation; see Menge and Lubchenco 1981, Robles and Robb 1993), or (2) total predation is slight (here termed "weak" predation).

Ultimately, the keystone predator concept will be most useful if many communities are characteristically controlled by such a species, particularly if keystone and nonkeystone predators (or their communities) have specific distinguishing characteristics. If such distinct and predictable properties were identified, the concept would have important theoretical implications and could be an invaluable tool in management and conservation of ecosystems (e.g., Bond 1993, Lawton and Brown 1993, Mills et al. 1993). For example, Paine (1969) suggested two important properties were (1) the predator preferentially consumed and controlled the abundance of a prey species, and (2) this prey species

could competitively exclude other species from the community. In the absence of such general, identifiable properties the concept would be less useful.

Variation in interaction strength

Mills et al. (1993) and Strong (1992) also consider a second issue: the variability of keystone predator effects, both within and between broad habitat types (i.e., marine, freshwater, terrestrial). For somewhat different reasons, both conclude a primary focus should be more on factors underlying variation in predation effects, or the strength of the interaction between predators and prey, than on a "keystone/non-keystone dualism" (Mills et al. 1993) or "true trophic cascades" (Strong 1992). Mills et al. (1993:223) explicitly advocate abandonment of the keystone species concept.

We believe this concept remains useful but agree that clarification is needed. Moreover, a focus on variation in interaction strength, here defined as the impact of one population on the distribution, abundance, and/or body size of another population of major importance in the community, seems important to further progress in ecology (e.g., see Menge and Sutherland 1987, Menge and Olson 1990). Evaluation of the issues of variation in interaction strength and the generality and importance of the keystone species concept will depend at least partly on developing a set of detailed multifactorial studies in a variety of communities and habitats. This assumes that, by studying how and why interactions vary in relation to factors such as environmental stress, recruitment, habitat complexity, or productivity, insight can be gained into both the importance of different types of interactions and the forces underlying their variability.

Determination of interaction strength depends on field experimentation (e.g., Paine 1980, 1992, Menge and Sutherland 1987, Mills et al. 1993). However, field manipulation of factors such as wave forces or temperature is usually unfeasible, and the spatial scale of experimentation may be limited (Diamond 1986). A useful technique in such cases is the "comparative experimental" approach (Menge and Sutherland 1987, Lubchenco and Real 1991, Menge 1991b), in which replicated, identically designed, controlled field experiments are done at different sites along environmental gradients. Nesting such experiments at different spatial scales, and repeating them through time, can indicate the importance and generality of the phenomena. Observations and measurements of relevant environmental conditions and comparisons among sites can provide insight into the importance of different factors varying along environmental gradients (for examples of this approach, see Dayton 1971, 1975, Menge 1976,

1978a, b, 1983, 1991a, b, Lubchenco and Menge 1978, Lubchenco 1986, Dethier and Duggins 1988).

Testing for keystone predation

Ideal tests for keystone predation should involve manipulation of both single species and the entire predator guild. Total removals/exclusions test for the overall strength of predation and serve as a reference for results of single species manipulations. Thus, for example, if (1) total predation was high, and (2) comparably large changes resulted from manipulation of one species but no others, then predation was keystone. Alternatively, if the total predation was due to two or more species whose combined effect was equivalent to total predation but separate effects were not, then predation was diffuse.

This ideal design has rarely if ever been employed, although some have tested the effects of total predation and of single functional groups of predators (e.g., Dayton 1971, Quammen 1984, Menge et al. 1986). Others compared total predation to estimated effects of single species based on field feeding rates (Menge 1983, Paine 1992). Generally, however, keystone predation was established from manipulations of single predators based on a priori knowledge of natural history (e.g., Paine 1966, 1971, 1974, Hall et al. 1970). The relative unimportance of other species was commonly inferred, primarily from dramatic community responses to manipulation but secondarily from evidence such as low abundance, small size, etc.

Generalizations have both between- and within-system contexts. That is, the generality of a concept (e.g., the keystone predation hypothesis) can be determined with respect to its applicability (1) across a variety of ecosystem types and (2) to different portions of a particular ecosystem type. In (1) we ask if keystone predator effects occur in communities in lakes, streams, deserts, mountainsides, rocky intertidal, kelp forests, etc. Affirmation from a variety of systems would suggest that the concept has broad generality and is thus ecologically important. In (2) we ask if a predator is a keystone species in a particular habitat (e.g., lakes), and if so, do its effects vary with depth, size, thermal regime, productivity, etc.? Such investigations would provide mechanistic insight into how the interaction varies with other environmental factors and thus help to specify the contingencies modifying its effects. Combining studies from both within and between habitats would be necessary to determine if keystone predators were a class apart or not.

This paper investigates keystone predation using the comparative-experimental approach in a rocky intertidal habitat with the primary goal of gaining a mechanistic understanding of the patterns and causes of variation in its community effects. The prototypical keystone predator, the seastar *Pisaster ochraceus*, was used to determine how and why its predation varied in relation to a variety of ecological processes and en-

vironmental conditions. In addition, we address the implications of our results in a broader, between-systems context.

BACKGROUND

On the outer coast of Washington state, predation by *Pisaster* eliminated mussels (*Mytilus californianus*) from the low rocky shore at two wave-exposed locations (Paine 1966, 1974). This set the lower distributional limit of the competitively dominant mussel and helped maintain a diverse assemblage of competitively subordinate seaweeds and invertebrates. This result, and similarities in species composition and zonation pattern at localities ranging from Baja California to Alaska, led Paine (1969) to propose that within this system, the *Pisaster*-*Mytilus* interaction controlled the structure of exposed rocky shore communities over a wide latitudinal range.

Paine's studies also produced two between-system generalizations: the keystone species hypothesis defined and discussed above, and the "predation hypothesis," which postulated a unimodal relationship between predation intensity and prey species diversity (Paine 1966). As noted by Mills et al. (1993), the effects expected under the predation hypothesis are often included among keystone predator effects. The two concepts are not necessarily interdependent, however, since the effects predicted by each can occur independently of the other (McCauley and Briand 1979, Hixon and Brostoff 1983, Menge et al. 1985, Hixon 1986, Menge and Sutherland 1987, Martinsen et al. 1990; see also Fuentes and Jaksic 1988). Examples of keystone predators have been suggested in all major habitats (e.g., Estes and Palmisano 1974, Carpenter et al. 1987, Kerbes et al. 1990, Estes and Duggins 1995), but so too have examples of strong predation without a keystone (Menge et al. 1986, Power 1990, Strong 1992, Robles and Robb 1993).

Some have questioned the within-system generality of Paine's (1966) results. Fairweather and Underwood (1983) argued that mussels may not have been truly preferred and thus doubted the importance of predation on dominant competitors in controlling the structure and diversity of intertidal communities. Foster (1990), citing surveys along the California coast showing spatial variation in mussel cover, suggested the keystone effect of *Pisaster* was not general (see Foster 1991 and Paine 1991 for further commentary). Underwood and Denley (1984) argued that recruitment had been neglected as an alternative determinant of community structure.

Under some conditions, *Pisaster* may have little or no effect on mussel distribution. For example, citing the near-absence of the seastar-preferred California mussel, Paine (1980) speculated that *Pisaster* was "just another seastar" in Torch Bay, Alaska. The blue mussel, *M. edulis* (reclassified for northern populations as *M. trossulus*; McDonald and Koehn 1988, McDonald

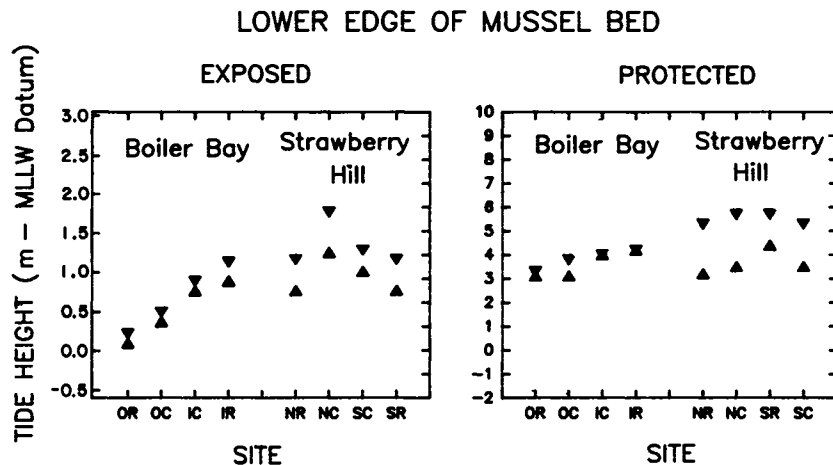


FIG. 1. Tidal level (distance above or below mean lower low water [MLLW] datum) of the lower edge of the *Mytilus californianus* bed at each experimental site. Data are the height above MLLW of the lowest (▲) and highest (▼) part of the edge within each experimental plot. Experimental plot codes at Boiler Bay: OR, outer removal; OC, outer control; IC, inner control; IR, inner removal. The arrangement of the plots corresponds to their actual arrangement, from wave-exposed (left) to wave-protected (right). Experimental plot codes at Strawberry Hill: NR, north removal; NC, north control; SC, south control; SR, south removal. The arrangement of the plots corresponds to their actual arrangement from north (left) to south (right).

et al. 1991), also favored by *Pisaster* (Landenberger 1968), was common, however. In another case, spiny lobsters, not seastars, were keystone predators of mussels in two habitats (high sheltered and mid exposed rocky shores) of Santa Catalina Island in southern California (Robles 1987, Robles and Robb 1993). Moreover, lobsters were only one of several (diffuse) predators collectively acting to control mussel abundance in a third habitat (mid sheltered shores; see Menge and Lubchenco 1981, Menge et al. 1986 for other examples of diffuse predation). In this study, both *M. californianus* and *M. edulis* (reclassified for southern populations as *M. galloprovincialis*; McDonald and Koehn 1988, McDonald et al. 1991) were naturally scarce and *Pisaster* were absent (Robles 1987). In summary, although few disagree with Paine's interpretations of his experiments, questions remain regarding (1) the conditions under which the effect occurs, and (2) their generality in space.

On the Oregon coast, observations begun in 1980 revealed high temporal and spatial constancy of the lower limit of the California mussel (B. A. Menge, *personal observations*). Moreover, mussels were limited to their mid zone refuge not only at wave-exposed sites but also at wave-sheltered sites (e.g., Fig. 1). This constancy occurred despite enormous spatial variation in *Pisaster* density. Especially at wave-sheltered areas, seastars were virtually absent for long periods of time, yet the lower limit of mussels did not change.

This system thus seemed ideally suited to an examination of both variation in the strength of this key interaction, and of the potential direct and indirect roles of alternative factors, in maintaining a persistent feature of community structure. Since seastars were relatively more abundant at wave-exposed sites, it

seemed likely that predation, either by *Pisaster* alone or with other predators, was still the major cause of low mussel abundance at such locations. Further, it was conceivable that even when scarce, *Pisaster* could keep up with increases in mussel abundance if such increases occurred slowly. Low recruitment or slow growth of mussels, or both, could underlie slow increases in mussel abundance. Thus, seastar predation could also be the primary determinant of the lower limit of mussels at sheltered sites.

Several alternative factors could also be important, however. Dayton's (1971) studies suggested that under some conditions, whelks could compensate for low seastar abundances and increase their influence on mussel abundance. Other predators are known to prey on mussels (e.g., fishes: Brett 1979; birds: Marsh 1986, Dittman and Robles 1991, Wootton 1993; crustaceans: Robles 1987) and their possible effects should be considered. In addition, low recruitment, intolerance of physical conditions, or pre-emptive competition by algal turfs could keep mussels from living low on the shore at sheltered sites.

Here, we report investigations of some of these issues. We sought to quantify both the intensity and community effect of *Pisaster* predation under varying environmental conditions. Results suggest that *Pisaster* predation varied dramatically at scales ranging from <10 m, to 10's and 100's of metres, and to 10's of kilometres, but, given time, was usually sufficient to eliminate mussels from the low intertidal. At wave-exposed areas, predation was consistently strong and predictably eliminated mussels from the low zone. In wave-protected areas, however, predation was both weaker and more variable in space and time, and other factors such as sand burial and low recruitment ap-

peared important. Our study provides mechanistic insight into the causes of variation in keystone predation and suggests that the scope of models of predator control of community structure should be expanded. Specific questions were:

- 1) What are relative contributions of predation and other factors to the spatial and temporal patterns of mortality of mussels in the low zone?
- 2) How important are alternative causes of mussel zonation such as other predators, sand burial, low prey recruitment, or the prior presence of an algal turf?
- 3) Under what conditions does *Pisaster* have a keystone effect?
- 4) What insights into the generality of the keystone predator concept are provided by our experiments and similar studies?

METHODS

Study sites

Studies were carried out primarily from 1989 to 1993 at two sites along the central Oregon coast, Boiler Bay and Strawberry Hill. Boiler Bay (44°50' N, 124°03' W; hereafter BB; see Turner 1985, Marsh 1986, Farrell 1988 for previous descriptions) is a convoluted stretch of rocky shore 1 km north of Depoe Bay. Studies were conducted on a linear series of three benches \approx 300 m in total length running northwest to southeast and separated by small (<5 m wide) channels. The benches sloped gently toward the southwest. A striking wave exposure gradient occurred along the benches. The seaward bench was exposed to severe wave forces for much of the year and was inaccessible during storms. The landward bench was more sheltered from wave forces and experienced only moderate turbulence during storms. The benches exhibited classic patterns of zonation, with a high intertidal zone dominated by fucoid algae (mostly *Pelvetiopsis limitata*) and barnacles (*Balanus glandula*), a mid intertidal zone dominated by mussels (*Mytilus californianus*), and a low intertidal zone dominated by a multispecific mosaic of seaweeds and surfgrass (Menge 1992, Menge et al. 1993).

Strawberry Hill (44°15' N, 124°07' W; hereafter SH; see D'Antonio 1985 for a previous description) is an extensive rocky bench \approx 80 km south of BB. Unlike the relatively uniform sloping benches of BB, the topography of SH consists of a complex mix of outcrops, pools, surge channels, and broad flat benches. As at BB, a striking wave exposure gradient occurs at SH. Heavy surf pounds the seaward edge of the site while wave forces are greatly diminished at the landward edge, \approx 200 m distant. Cliffs ranging from \approx 50 m (SH) to \approx 100 m (BB) rise up from the landward edge of each site.

Community structure

Despite broad similarities, patterns of zonation and low intertidal community structure at SH differed from

those at BB. Most obviously, seaweed cover appeared lower and both vacant space and sessile invertebrate cover appeared higher at SH than at BB (Menge 1992). The transect-quadrat method was used to quantify these patterns (for details, see Menge 1976, Lubchenco et al. 1984). Percent cover and/or numerical density of all organisms occurring within 10–15 quadrats, each 0.25 m² in area, was sampled at either random or regular intervals along a transect line. Such samples were taken irregularly at each site and location. The most complete data sets are presented in Figs. 2 and 3.

Pisaster population structure.—Seastar densities were estimated in large plots in 1990. Plot area was determined by measuring the distance from a central point in each plot to the perimeter at 5°–15° intervals around the center (e.g., Menge 1972). These measurements were plotted on polar coordinate graph paper and the enclosed area measured with a digitizer. Dividing number of seastars present (or removed; see below) by area gives average density for each plot.

For comparison, seastar density estimates from previous studies are included in Fig. 4. All of these estimates were gathered (by the original authors cited in the caption of Fig. 4) using essentially the same method: the number of *Pisaster* counted at a site (e.g., in a "belt" transect, or strip of shore 1–2 m wide and 10–30 m long) was divided by the total area (in square metres) surveyed.

To compare seastar sizes among the different sites or treatments, field populations were sampled. For seastars, wet mass and ray length were measured for \leq 200 individuals in half of the large plots, yielding two samples of size structure at each combination of wave exposure and site. Sample sizes per plot were small at all locations except SH exposed, however, so samples were pooled to provide single representations of size structure for each of the two sites. Wet mass (in grams) was measured using a spring scale; ray length (in millimetres) was the distance from the madreporite to the tip of the opposite arm.

Experimental design

One means of determining the effect of relatively mobile, large-bodied predators is to remove or exclude them and observe the response of the rest of the community (e.g., Connell 1961, Paine 1966, Dayton 1971, Menge 1976, Fairweather 1985, Dungan 1987). Depending on colonization and growth rates, results from such experiments can be obtained in months to years. Differences between abundance of prey in the absence vs. the presence of predators have been used as estimates of predation effect (e.g., Menge 1978a, 1983, Paine 1992). However, if recruitment is sporadic, removal/exclusion experiments have an element of uncertainty: how long should one wait to be sure results are in some sense complete? A complementary approach estimates the intensity, or rate of predation. Instead of waiting for prey to colonize, one estimates

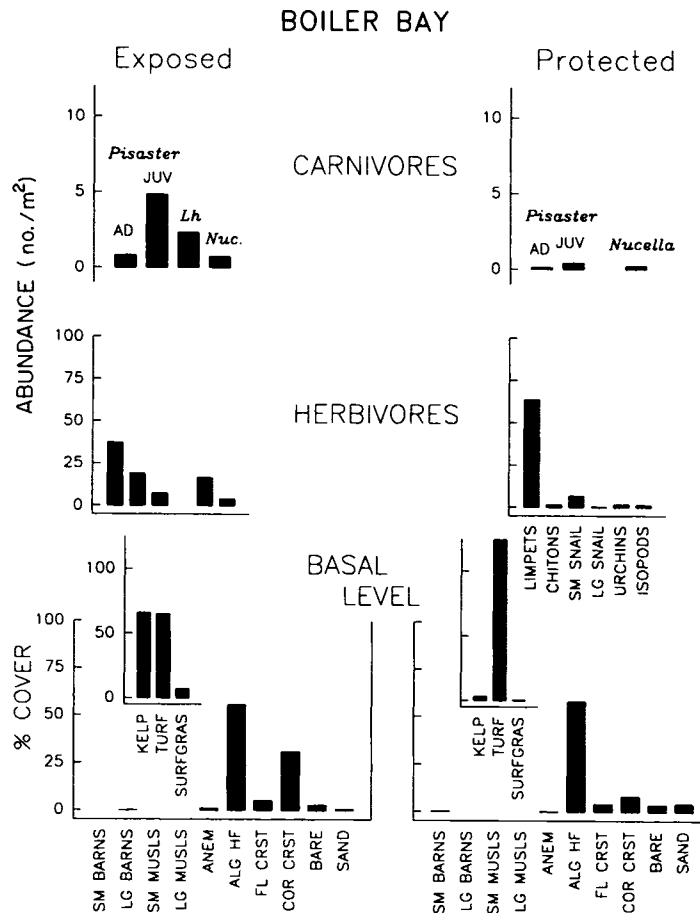


FIG. 2. Summary of abundances of carnivores, herbivores (number/m²), and sessile organisms (basal level, percent cover) at wave-exposed (sampled July 1981) and wave-protected (sampled July 1983) sites in the low zone at Boiler Bay, Oregon. Sessile organisms are presented as occupiers of primary space (lowest axes) and canopy space (inset axes). Data were collected using the transect-quadrat method (see Lubchenco et al. 1984), and are the average of abundances in 10–15 quadrats, each 0.25 m² in area. Codes for abscissa: CARNIVORES include: adult (AD) and juvenile (JUV) *Pisaster ochraceus*, *Leptasterias hexactis* (Lh), and *Nucella* spp. (Nuc). HERBIVORES include: *Lottia* spp. (LIMPETS), *Katharina tunicata* and *Tonicella lineata* (CHITONS), *Littorina* spp. and *Lacuna* sp. (SM SNAILS), *Tegula funebris* (LG SNAILS), *Strongylocentrotus purpuratus* (URCHINS), and *Idotea* spp. (ISOPODS). Animal occupants of primary space (BASAL LEVEL) include: small barnacles *Chthamalus dalli* and *Balanus glandula* (SM BARN), large barnacles *Semibalanus cariosus* and *Balanus nubilus* (LG BARN), small mussels *Mytilus trossulus* (SM MUSLS), large mussels *M. californianus* (LG MUSLS), and anemones *Anthopleura elegantissima* and *A. xanthogrammica* (ANEM). Plant occupants of primary space are algal holdfasts (many species; ALG HF) and crustose algae (fleshy species such as *Hildenbrandia* sp. and *Petrocelis* sp., termed FL CRST and many calcareous species, termed COR CRST). BARE is vacant space and SAND is rock surface covered by sand. Canopy space occupants include *Hedophyllum sessile* and *Lessoniopsis littoralis* (KELP), many species of foliose algae (TURF), and *Phyllospadix* spp. (SURFGRAS). Axis labels for herbivores are shown only for the protected site but are the same for the exposed site.

the mortality rate of prey transplanted to areas with or without predators (e.g., Kitching et al. 1959, Menge 1978b, 1992, Garrity and Levings 1981, Aronson 1989). This technique both avoids the potentially confounding effects of spatial and temporal differences in prey recruitment density and growth and provides a standardized estimate of the intensity of predation between seastars and mussels. Because such experiments do not incorporate rates of prey supply (recruitment, growth), they can be viewed as providing an estimate of “potential” interaction strength. Both approaches were used in this study.

Predation intensity: mussel transplant experiments.—To estimate the rate of predation on mussels, adult *M. californianus* of 4–7 cm shell length were collected from the mid-intertidal at each location and transplanted to the low zone (below the mussel bed) in clumps of 50 mussels each. *Pisaster* effects were tested by establishing clumps within large plots with (controls) and without (experimentals) seastars.

To mimic their orientation in natural mussel beds, individual mussels were placed in overlapping rows with the ventral side against the rock. Clumps were held against the rock with cages of Vexar plastic mesh

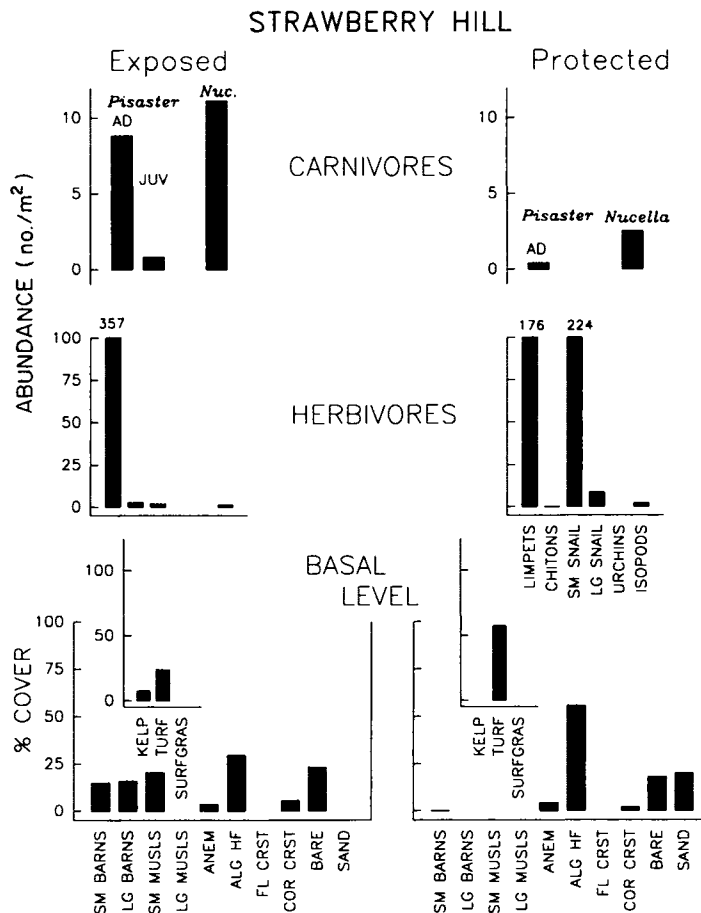


FIG. 3. Summary of abundances of carnivores, herbivores, and sessile organisms at wave exposed and wave protected (both sampled April 1990) sites in the low zone at Strawberry Hill, Oregon. See Fig. 2 caption for further details.

(Fig. 5) to allow them to reattach byssal threads to the rock. Most had reattached within days, but clumps were caged for about a month to allow firmer attachment and reduce potential losses due to waves. Paine (1976) used a similar method to transplant mussels in Washington state.

The experimental design included two locations (BB and SH) \times two wave conditions (exposed and protected) \times two *Pisaster* treatments (present and absent, or + and -) \times two replicates (Fig. 5). Each replicate consisted of two large plots adjacent to one another in the low intertidal (separated by 1–10 m). Large plots ranged in area at BB from 72 to 105 m² (controls) and 33 to 130 m² (removals) and at SH from 18 to 90 m² (controls) and 69 to 163 m² (removals). Plot size varied as a function of substratum discontinuities used to delineate each. All plots were sufficiently large for transplant clumps and marked quadrats (see below) to fit with room to spare. All had a bed of California mussels at the upper edge.

Ten mussel clumps were transplanted to each large plot, yielding a nested design (clumps were subsamples nested within replicates). *Pisaster* were manually re-

moved from one of the paired large plots and counted but otherwise not disturbed in the other. Assignment of *Pisaster* treatments among paired plots was random at SH, but at BB depended on local topography and logistics of seastar removal. Location of plot pairs within exposures at each site was based on topography and similarity of community structure. At BB, for instance, plot pairs were located on sections of the intertidal benches separated by substratum discontinuities such as crevices or channels. At SH, plot pairs were located on outcrops separated by shallow surge channels or broad benches.

Low intertidal rock surfaces at BB were almost completely covered by macrophytes (Menge et al. 1993; Fig. 2). These plants formed a dense turf \approx 5–10 cm thick, often completely obscuring the rock surface. Dominant species were *Constantinea simplex*, *Dilsea californica*, *Cryptopleura* spp., *Hymenena* spp. (all wave-exposed); *Neorhodomela larix*, *Odonthalia floccosa* (wave-protected); and the surfgrass *Phyllospadix scouleri* (both exposed and protected). Since the turf might affect mussel survival (e.g., by preventing firm attachment, interfering with predator feeding, and/or

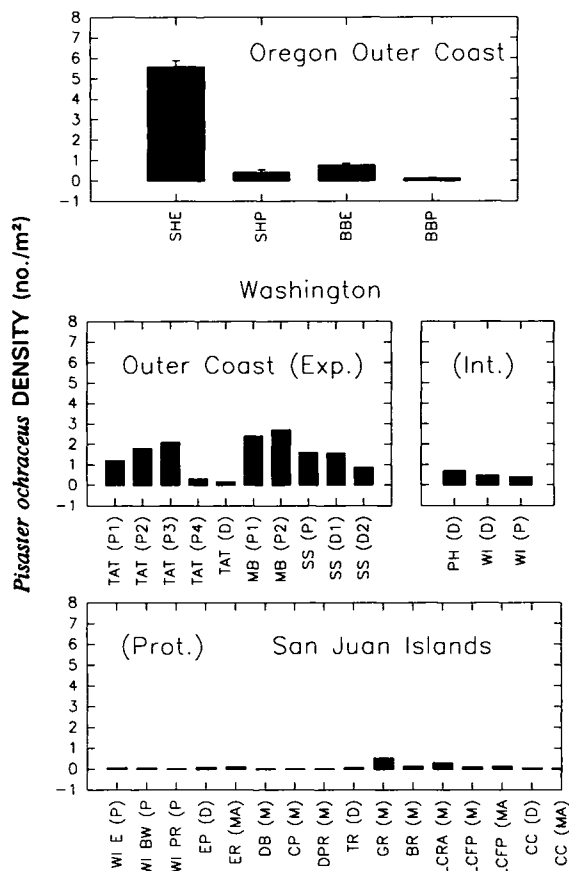


FIG. 4. Density of *Pisaster ochraceus* at sites in Oregon (top) and Washington (middle and bottom). Oregon site codes: SHE, Strawberry Hill exposed; SHP, Strawberry Hill protected; BBE, Boiler Bay exposed; BBP, Boiler Bay protected. Density estimates that could be assigned to one of three wave-exposure categories (Exp., wave-exposed; Int., intermediate wave exposure; Prot., wave-protected) were obtained from several literature sources and were coded (in parentheses) as follows. Paine 1974: two from Tatoosh Island [TAT (P1) and TAT (P2)] and two from Mukkaw Bay [MB (P1) and MB (P2)]. Paine 1976: two from Tatoosh Island [TAT (P3) and TAT (P4)], one from Shi Shi Beach [SS (P)], and four from Waadah Island [WI (P), WIE (P), WIBW (P), WIPR (P)]. Dayton 1971: two from Shi Shi Beach [SS (D1), SS (D2)], and one each from Tatoosh Island [TAT (D)], Portage Head [PH (D)], Waadah Island [WI (D)], Eagle Point [EP (D)], Turn Rock [TR (D)], and Colin's Cove [CC (D)]. Mauzey 1967: one each from Edward's Reef [ER (MA)], Lonesome Cove Far Point [LCFP (MA)], and Colin's Cove (CC (MA)). Menge 1972: one each from Deadman Bay [DB (M)], Cattle Point [CP (M)], Lonesome Cove Resort Area [LCRA (M)], and Lonesome Cove Far Point [LCFP (M)]. Menge 1974: one each from Davis Point Reef [DPR (M)], Gull Reef [GR (M)], and Buoy Reef [BR (M)]. Tatoosh Island, Mukkaw Bay, Shi Shi Beach, Portage Head, and Waadah Island are all sites on the outer Washington coast. Eagle Point, Edward's Reef, Deadman Bay, Cattle Point, Davis Point Reef, Turn Rock, Gull Reef, Buoy Reef, Lonesome Cove Resort Area, Lonesome Cove Far Point, and Colin's Cove are all sites in the San Juan Islands.

hindering seastar attack), this potential effect was tested as well.

In 1990, five mussel clumps were transplanted to cleared (BB) or naturally bare (SH) rock and five clumps were transplanted to turf-covered rock in each large plot. Turf treatments were assigned within plots at random. In 1991, no turf treatment was included because no turf effect was detected in the 1990 experiment (see below). Experiments were initiated in mid-June each year by removing the mesh cages from mussel clumps in both +*Pisaster* and -*Pisaster* treatments. The response (dependent) variable was the number of mussels alive per clump on each sample date. Mussels were counted and seastars removed at each site on consecutive days at intervals of ≤ 14 d until mid-September (1990) or early October (1991), when poor tides and/or bad weather prevented continuation of frequent visits, effectively terminating the experiment. This was thus a "press" manipulation (Bender et al. 1984:2). Thereafter, seastar removal was done whenever possible to maintain the treatments testing for longer term seastar effects.

In addition to counting the number of mussels alive per clump and removing invading *Pisaster* during each sample period, the number of clumps with *Pisaster* present and actively feeding were counted. In *Pisaster* removal plots, large mussel losses occasionally occurred in individual clumps. Some of these losses were clearly due to foraging by reinvading seastars, indicated by either direct observation of seastars feeding on a clump or the nearby presence of seastars clinging to the shells of consumed mussels. Such clumps were dropped from subsequent calculations of mussel survival. Clumps with losses that could not be attributed to seastars were included in calculations, although it is likely that most such losses were in fact due to seastar predation. If fewer than 3 (of 10 original) uninvaded clumps were available in -*Pisaster* plots for a particular sample date, the replicate was dropped thereafter from calculations.

We emphasize that by removing only *Pisaster* and leaving other predators present, the effect of the seastar alone was tested directly at each location \times wave exposure combination. Thus, if survival of transplanted mussels was significantly greater in experimental plots (-*Pisaster* + other predators) than in control plots (+*Pisaster* + other predators), *Pisaster* alone was responsible for the difference. The magnitude of the difference, if any, should indicate the strength of the effect. Small to moderate differences between treatments would suggest *Pisaster* had no keystone effect, while large differences would suggest *Pisaster* may have a keystone effect.

In one case (SH protected), survival of transplanted mussels did not differ between treatments, but was low overall. Transplants established in June 1991 at each site \times exposure combination tested if low survival was due to other predators. In this experiment, cages were

DESIGN: MUSSEL TRANSPLANT EXPERIMENTS

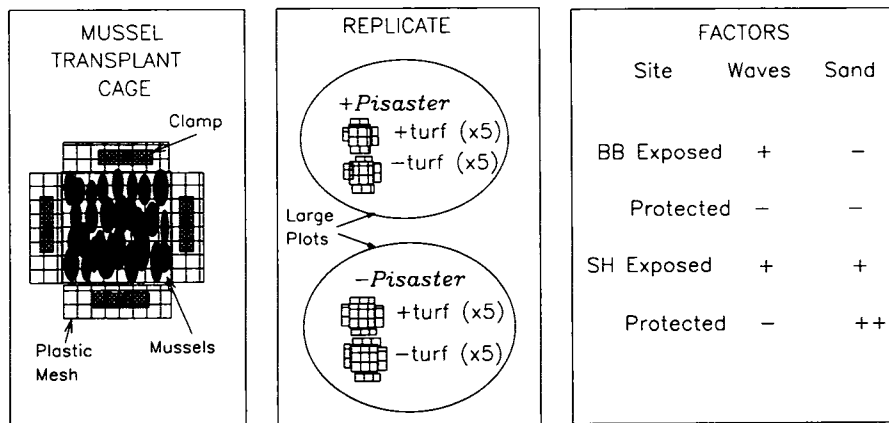


FIG. 5. Diagram of the design of mussel transplant experiments. Left box: diagram of a mussel transplant cage (dimensions of mussel containment area, 20 × 20 cm). The cage is held down by screws through clamps on the four edge flaps of the mesh cage. Middle box: diagram of a replicate, each consisting of two large plots, one with and one without *Pisaster*. Large plots ranged in area from 18 to 163 m². Each large plot contained 10 transplanted mussel clumps. In 1990 but not 1991, five clumps were placed on algal turf and five were placed on vacant rock surfaces. Right box: factors varying among the site × exposure combinations (two replicates = four large plots for each combination) were waves (+, wave-exposed; -, wave-protected) and sand. Sand was negligible (-) at Boiler Bay, present but never buried rock surfaces (+) at Strawberry Hill exposed, and present and frequently buried rock surfaces (++) at Strawberry Hill protected. Proportion of mussels surviving per clump was the dependent variable.

left in place instead of removing them after the mussels had reattached. Since the cages excluded all large predators (seastars, crabs, birds, fishes), survival differences should be due to factors other than predation by these organisms.

At most site × exposure combinations, mussels were completely absent from the low zone, with the occasional exception of isolated large *M. californianus* that had evidently reattached after being dislodged from mussel beds higher on the shore. At SH exposed, however, *M. trossulus* was seasonally abundant in the low zone. Field observations of seastars consuming these smaller mussels left little doubt regarding the cause of their annual summer decline in abundance. To test this effect, similarly designed experimental transplants of *M. trossulus* (1.5–3.5 cm in length) were done in summer 1992 (after the decline of *M. trossulus* abundance).

Predation effect: prey and community responses.—Two studies determined the long-term effect of predation on community structure. First, in each large plot 12 20 × 20 cm quadrats were established by marking them at the corners with stainless steel screws. Also, to determine if prior occupants influenced colonization events, six of the quadrats were selected at random and cleared of organisms using scrapers. Marked quadrats were photographed four times (June 1990, January/February, May/June, and August 1991) to monitor changes in prey abundance. Abundance of sessile organisms (percent cover) was estimated from the photographs using transparent vinyl random dot sheets (Connell 1961, Dayton 1971, Menge 1976).

Second, to determine the long-term effect of *Pisaster*

on *M. californianus* colonization in the low zone, each large plot was periodically photographed and observations were made of the position of the lower edge of the mussel bed in relation to local landmarks. Changes (both lateral and vertical distance moved) occurring since experiment initiation in spring 1990 were estimated in March 1993.

To quantify the similarity of the large plots before manipulations were initiated, and determine the effects of *Pisaster* on abundance of mobile species, densities were estimated in each plot before and 12 mo after manipulations were begun using the transect–quadrat method (see above). Initial abundance of sessile organisms was determined from the photographs of marked plots (see above).

Because their diets are similar to those of seastars, whelks are the consumer species most likely to respond to *Pisaster* removal. In addition to density changes (see above), differences in size structure of *Nucella canalculata* in the presence and absence of *Pisaster* were also quantified. Shell length (in millimetres) was measured as the distance from the end of the siphonal canal to the tip of the shell spire. *Nucella* size was sampled only in the four wave-exposed large plots at Strawberry Hill in June 1991, 1 yr after seastar removal had begun, because field observations indicated whelk size had changed dramatically in these and no other plots.

Mussel recruitment.—Two methods of estimating mussel recruitment were considered; samples from natural substrata (e.g., Paine 1974) or samples from artificial substrata (e.g., Menge 1978b, 1991a). Sampling natural substrata offered the advantage of providing

estimates of actual recruitment, but the disadvantages of impracticality and inability to quantify temporal recruitment patterns accurately. For instance, obtaining estimates unbiased by either substratum heterogeneity or variable larval substratum preferences would be inordinately time consuming and costly. Paine's (1974) observation of tremendous variation in mussel recruitment (range: 0–40 000 mussels/m²) among nine different substrata allows some estimates. A monthly sampling scheme involving five replicates of nine substrata at two tidal levels, two wave exposures, and two sites would generate 360 samples. Assuming (probably unrealistically) that each took only 1 h to sort, sample processing would require 2.25 full-time counters. Using a single (artificial) substratum with an otherwise identical design would generate only 40 monthly samples requiring 0.25 counters.

Sampling natural substrata would also obscure temporal patterns of recruitment. Assuming each sample was obtained from a new surface each month, distinguishing recently settled mussels from those settling in previous months would be difficult, especially during periods of little or no growth. Since we sought information on the timing and intensity of recruitment, samples from natural surfaces appeared unsatisfactory.

Artificial substrata are virtually identical and should thus minimize variation due to microtopographic heterogeneity; larval preference; or size, density, and condition of living substrata, thereby permitting a clearer estimate of variation in time and intensity of recruitment. However, recruitment density estimates so obtained are "relative," not "absolute." Thus, while recruitment estimates from artificial substrata can be analyzed in the context of the sampling scheme (e.g., we could evaluate if recruitment to surfaces was higher at exposed than protected sites, or higher at mid-shore levels than at low-shore levels, etc.), they did not necessarily estimate "natural" recruitment densities.

Artificial substrata used for estimating mussel recruitment were plastic mesh dish scrubbers ("Tuffies"), here termed "collectors." Beginning in August 1989 (mid zone) and September 1991 (low zone), five collectors were fastened to areas of bare rock at each combination of site \times exposure \times tide level and were replaced monthly. These devices mimicked the physical structure of filamentous substrata such as the alga *Endocladia* and mussel byssal threads, surfaces apparently preferred for settlement by mussel larvae (Bayne 1964, Paine 1974, Seed 1976). Observations made monthly checked if high recruitment densities in collectors were eventually (i.e., within 2–3 mo) reflected in the appearance of small mussels on the shore.

Mussel recruit abundance was determined by opening and flattening each collector over a 20 \times 20 cm vinyl sheet subdivided into a 5 \times 5 grid of 4 \times 4 cm subquadrats. The flattened collector was scanned under a dissecting microscope. If mussels were abundant (several hundred to thousands per collector), counts

were made in five 4 \times 4 cm subquadrats on the diagonal. If mussels were scarce, counts were made in the entire collector. Numbers were expressed as individuals per 100 cm².

Mussels < 1 mm cannot be reliably identified, so the specific status of the mussel recruits was uncertain. *Mytilus trossulus* are generally the most numerous mussels colonizing clearances in mussel beds (Paine and Levin 1981, Sousa 1984; B. A. Menge et al., *personal observations*) so the majority of recruits were probably blue mussels. However, in a separate but nearby study, observations made 1.5–2.5 yr after initial recruitment indicated 34.6% (of 162) mussels in 16 mid-zone predator-exclusion cages were *M. californianus* (E. Berlow, *unpublished data*), suggesting both species recruited.

Mussel growth.—Mussel growth was estimated at each site \times exposure combination. In June 1991, mussels surviving the first (1990) mussel transplant/seastar predation experiment were collected. The mussels produced a distinct ridge or checkmark at the shell edge after transplantation, so measurement of the shell added after the checkmark provided an estimate of individual growth during 1990–1991. In 1991, mussels marked with individual tags glued to the shell were measured, then transplanted and left in cages (30 mussels per each of 5 cages per site \times exposure) to reduce losses to predators. Individual growth during 1991–1992 was estimated after collecting these mussels in June 1992.

Data analysis

Data analyses employed SAS (Release 6.03; SAS Institute 1988) and SYSTAT (Release 5.0; Wilkinson 1990) statistical packages for IBM-compatible PCs. In the mussel transplant experiments, estimates of survival were clearly correlated over time, so results were analyzed using a nested repeated measures analysis of variance (RM-ANOVA). Survival of mussels on successive sample dates were the "repeated measures" (dependent variables). Data from both the 1990 and 1991 experiments did not exhibit homogeneity of treatment differences variance ("compound symmetry"; Gurevich and Chester 1986, Mead 1988), as tested by the sphericity test using Mauchly's criterion (Crowder and Hand 1990). This precludes use of a standard univariate split-plot approach to analyze the within-subject hypotheses (i.e., time and its interaction with the treatments; Mead 1988). In these cases, we present both the adjusted Huynh-Feldt probability values (for univariate tests) as well as the results of multivariate analysis of variance (MANOVA). The between-subjects analysis (main treatments and their interactions) was based on a three-way factorial design (site, exposure, and *Pisaster* as treatments) with two replicates (pairs of large plots) and with nested observations (mussel transplant clumps) within replicates (10 clumps per large plot). All three main treatments were consid-

ered as fixed effects and replicates and plots as random. Thus, tests of hypotheses for both main effects and interaction terms used the experimental error due to replicates (with 8 df, see Table 2) rather than the error due to clumps (which would be "pseudoreplicates"; Hurlbert 1984; see Snedecor and Cochran 1989, Chapter 16 for procedures in selecting the correct error term). The error due to clumps within replicates was used to test for differences among replicates.

Considering "site" as a fixed effect requires further explanation. As stated in the *Introduction*, the two sites (BB and SH) were chosen because they exhibited clear differences in community structure (Figs. 2 and 3; Menge 1992, Menge et al. 1993). They were clearly not chosen at random from a set of potential study sites. Further, we do not pretend to make statistical inferences about "sites" on the Oregon coast from this limited (only two sites) experiment. Instead, we use this and previous studies conducted elsewhere (e.g., Washington) with basic ecological knowledge of intertidal systems to suggest the generality of our results along the west coast of North America.

In the caged transplanted mussel experiment, survival was determined only once at the end of the experiment. These data were analyzed with a three-way (univariate) ANOVA, with site, exposure, and tidal level regarded as fixed factors. In this case, each transplanted clump of 30 mussels was a replicate, since the design included no nesting.

The effect of seastar predation on abundance of mussels in marked plots was analyzed only at the SH exposed site because no mussels colonized plots at other sites during this study. A repeated measures ANOVA was also used in this analysis to take into consideration the serial time correlation of the data. In this case, the design was a split plot, where *Pisaster* (presence or absence) was the larger, "between-plot" treatment, and turf (presence or absence) was the smaller, "within-plot" treatment. Both treatments were considered as fixed and the appropriate error terms to test main hypotheses and interactions are presented in the results (see Table 7). Data from this experiment exhibited compound symmetry (see above). Therefore, a standard split-plot approach with nonstandardized probability values was used for all the within-subjects hypotheses (see above). Multivariate ANOVA results are also presented for comparison. Split-plot ANOVA was also used to analyze the turf effect in the 1990 mussel transplant experiments.

Two-way ANOVA, with sites and exposures as fixed factors, was used to evaluate differences in mean individual mussel growth rates. Finally, ANCOVA with *Pisaster* ray length as the covariate was used to determine if regressions of wet mass \times ray length differed between SH and BB.

Percent cover data from marked plots and proportions of mussels surviving in mussel transplants were arcsine-transformed (Sokal and Rohlf 1981). Mussel

growth data were log-transformed prior to analysis. To determine if residuals were normally distributed and if errors were independent, probability plots of residuals and plots of residuals against estimated values, respectively, were examined visually (Wilkinson 1990). These assumptions were violated only by data from the initial sample dates in all experiments and on the last sample date in the 1991 transplant experiments. These dates were thus dropped from the analysis. In mussel growth analyses, outliers were dropped until normality and independence of errors was evident. Although this procedure did not change the statistical conclusions in any analysis, the analyses reported below were done on these reduced data sets.

Bartlett's test, the F_{\max} test (Sokal and Rohlf 1981), and Cochran's C test (Winer et al. 1991) indicated that variances of treatment groups were sometimes unequal, so the results of the RM-ANOVA (mussel transplants) and the two-way ANOVA (1990 mussel growth) must be regarded cautiously. Analysis of variance is generally little affected by violation of this assumption, however, as long as differences among variances are not too extreme (Day and Quinn 1989, Underwood 1981). Unequal variances among groups also precludes doing unplanned comparisons of means (Day and Quinn 1989), so date-by-date analyses of variance, with Bonferroni-adjusted probabilities, were used in conjunction with the plotted results to suggest which effects were significant and when differences occurred.

RESULTS

Community structure

As we observed, BB was plant dominated and SH was sessile invertebrate dominated (Fig. 2). In the low zone at BB, kelps (*Lessoniopsis* and *Hedophyllum*) and algal turf co-dominate space at the exposed area. Kelp abundance was low and turf abundance was high at the protected area, but plant cover was still $>100\%$ (due to layering). Abundance of barnacles and mussels was very low at BB regardless of exposure, and the cover of sand and availability of bare rock were both low as well. At higher trophic levels, abundance of limpets (*Lottia* spp.) and large snails (*Tegula funebris*) was higher at the protected site, while other herbivores (primarily chitons and sea urchins) were more abundant at the exposed site. In comparison to other sites on the Oregon coast, however, none of these herbivores would be considered particularly abundant at either area (B. A. Menge, *personal observations*).

Similarly, the carnivores (adult *Pisaster*, the seastar *Leptasterias* spp., whelks *Nucella* spp.), although more abundant at the exposed area, were not especially abundant at either exposure when compared to other locations in Oregon. Juvenile *Pisaster* (≤ 5 cm in diameter) were an exception; they were abundant at the exposed area (Fig. 2) and have been every year since observations were begun at this site in 1980 (B. A.

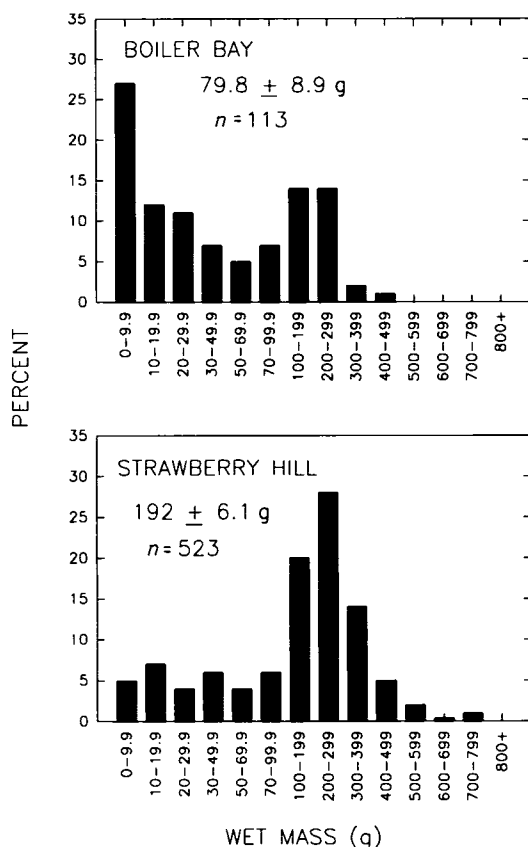


FIG. 6. Size structure (wet mass) of *Pisaster ochraceus* at Boiler Bay and Strawberry Hill. Mean \pm 1 standard error of the mean and sample size are given in each panel.

Menge, *personal observations*). Based on earlier work (Menge and Menge 1974, Menge 1975), we assume that juvenile *Pisaster* recruited sometime during the 12 mo prior to each sample.

At SH, patterns of low zone community structure display striking differences from those at BB (Fig. 3). Plant cover was relatively low, especially at the exposed area. Cover of barnacles and mussels was relatively high at the exposed area (peak covers are usually reached in February and decline thereafter to near zero in July–August; B. A. Menge et al., *personal observations*). Availability of bare rock was relatively high at both exposed and protected areas. However, the protected area differed from the exposed area in having a higher cover of sand and virtually no cover of mussels or barnacles.

At higher trophic levels, limpets (both exposed and protected areas) and small snails (mostly *Littorina scutellata*; protected area) were abundant (Fig. 3) but small (B. A. Menge et al., *unquantified personal observations*) at SH. No other macroherbivores were particularly abundant at either exposure (microherbivores such as amphipods were not counted). Carnivores (*Pisaster* and *Nucella* spp.), however, were very abundant at the exposed area. These species were less abundant at the

protected area, although whelks were still relatively abundant compared to BB.

Transect data from other years (not shown) and unquantified observations provide a temporal perspective to the static patterns shown in Figs. 2 and 3. Two striking differences between BB and SH were seasonal changes in the cover of mussels (*M. trossulus*) and sand. Every year from at least 1987 to 1993, the abundance of *M. trossulus* in the exposed low zone at SH increased from fall to spring, and then decreased. Mussel cover reached 100% over large areas of shore. At more sheltered sites at SH, large areas of rock were covered by sand from late summer to late autumn every year (see also D'Antonio 1985). Sand depth was often > 1 m at these locations. No such fluctuations in sand and mussel cover occurred at BB; both were scarce in the low zone at this site year-round. We stress, however, that apart from these repeatable annual changes, no other major changes were observed at either site for > 10 yr.

The differences in seastar abundance shown in Figs. 2 and 3 were reflected in independent estimates obtained at each location \times exposure in summer 1990 (Fig. 4, top). Densities were highest at wave-exposed sites, and higher at SH than at BB (two-way ANOVA on log-transformed data; 1, 12 df; $P < 0.0001$ for both main effects; the interaction was not significant). Average densities at SH exposed were 7.3 times those at BB exposed, the next densest site. Moreover, densities at SH exposed were higher than any *Pisaster* density recorded elsewhere (Fig. 4). Seastar density differences among sites and exposures appear consistent through time, as suggested by the number removed from each replicate from June 1990 to March 1992 (Appendix).

Pisaster size structure

Pisaster were on average twice as large at SH as they were at BB (Fig. 6). The primary difference was that many more small individuals < 50 g wet mass occurred at BB than at SH, although large (> 500 g) individuals were also absent at BB and present at SH. The relation between linear size dimensions (ray length) and body mass also appeared to differ significantly between sites (Table 1). Both the slopes and intercepts of the regressions were different (the site \times ray length [covariate] interaction is significant in the ANCOVA; Table 1). We do not consider these to be ecologically significant differences, however, since they are most likely due to the greater proportional representation of small (< 10 g wet mass) individuals at BB than at SH (Fig. 6) rather than a true allometric difference in seastars at the two sites.

Predation intensity: mussel transplant experiments

In 1990, survival of transplanted *M. californianus* was generally lower in the presence than in the absence of *Pisaster* (Fig. 7). Overall, the effect of *Pisaster* was strong but varied with exposure (Table 2; under “Be-

TABLE 1. Regressions between ray length and wet mass of *Pisaster* sampled at Boiler Bay and Strawberry Hill.

Site	Regression	R^2	n	P	\bar{X} mass (g)	\bar{X} ray length (cm)
Boiler Bay	$\ln \text{ wet mass} = -1.117 + 2.68 \ln \text{ ray length}$	0.983	113	<0.0001	79.8	6.3
Strawberry Hill	$\ln \text{ wet mass} = -0.728 + 2.51 \ln \text{ ray length}$	0.960	523	<0.0001	192.1	9.9
ANCOVA (H_0 : regression slopes are equal)						
Source	df	MS	F	P	R^2	
Site (BB vs. SH)	1	1.55	26.26	<0.0001		
Ray length (covariate)	1	1045.17	17707.7	<0.0001		
Site \times ray length	1	1.12	18.99	<0.0001		
Error	632	0.059			0.974	

tween subjects," the exposure \times *Pisaster* interaction was significant). Mussel mortality varied over time with site and exposure (Table 2; under "Within subjects," the time \times site \times exposure interaction was significant), and among some replicates (Table 2; replicate interactions were significant). Multivariate and univariate (within-subject) results were generally consistent, lending confidence to our interpretations.

The time course of mortality suggests predation intensity was greatest at SH exposed. Specifically, after exposure to predation at SH exposed, nearly all mussels were killed within 2 wk. At BB exposed and at both protected sites, mussel survival was much higher, at least initially (Fig. 7). Once the transplanted mussels were located by seastars at BB exposed, however, mortality increased sharply (B. A. Menge et al., *personal observations*). Mortality was consistent between replicates at the wave-exposed sites, but by the 23rd d mortality patterns in protected replicates diverged (Fig. 7, Table 3). Overall, mortality was significantly higher at exposed sites than at protected sites throughout the duration of the experiment (Table 2; multivariate repeated measures analysis).

The differences between replicates were most pronounced at protected sites, especially SH. At each site, mortality in one of two plots with *Pisaster* present (+*Pisaster*) was high while in the other +*Pisaster* plot, mortality was low and indistinguishable from that in -*Pisaster* plots (Fig. 7). Moreover, mortality rates varied greatly among transplant clumps within plots as well (Fig. 8). In other words, mussel survival varied significantly at protected sites on scales of metres (among clumps) to 10's of metres (between plots). Field observations indicated that part of this variation was due to seastar behavior and scarcity. When seastars were sparse, as at protected sites (Fig. 4), months sometimes passed before transplants were located. Upon discovery, however, the seastar would eat all mussels in the clump, while nearby undiscovered clumps had high survival. Overall, in 1990, predation intensity was high at wave-exposed sites, low but variable at wave-sheltered sites, and higher at SH than at BB.

In 1991, similar results were obtained (Fig. 9, Table 4). Mussel survival was poor in the presence of *Pisaster*, and differed with site and exposure (Table 4; under "Between-subjects," site \times exposure \times *Pisaster* interaction was significant). Survival varied through time and was influenced by all factors, either as main effects or in interactions. Differences due to each factor were

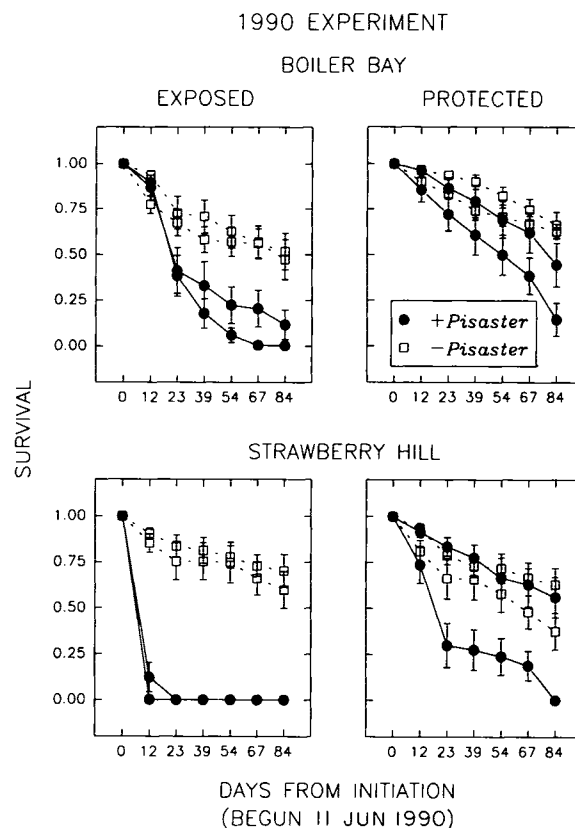


FIG. 7. Results of 1990 mussel transplant experiment. Data are proportion of *Mytilus californianus* surviving (mean \pm 1 SE; $n = 10$) for each replicate of two +*Pisaster* and two -*Pisaster* plots at each site \times exposure combination. The experiment was begun 11 June 1990 by removing the plastic mesh cages from the mussels.

TABLE 2. Repeated-measures nested analysis of variance on the effect of site, exposure, and seastar predation on mussel survival after 12, 23, 39, 54, 67, and 84 d in summer 1990.*

Source of variation	df	MS	F	P
Between subjects				
Site	1	4.50	2.16	>0.10
Exposure	1	17.3	8.29	<0.025
<i>Pisaster</i>	1	42.0	20.1	<0.005
Site \times exposure	1	0.023	0.011	>0.50
Site \times <i>Pisaster</i>	1	3.81	1.83	>0.10
Exposure \times <i>Pisaster</i>	1	12.8	6.12	<0.05
Site \times exposure \times <i>Pisaster</i>	1	4.04	1.94	>0.10
Replicate (site \times exposure \times <i>Pisaster</i>)	8	2.086	4.62	<0.0001
Error	115	0.451		
Within subjects				
Time	5	4.69	81.0	<0.0001
Time \times site	5	0.379	6.54	<0.005
Time \times exposure	5	0.153	2.65	>0.05
Time \times <i>Pisaster</i>	5	0.377	6.51	<0.005
Time \times site \times exposure	5	0.412	7.12	<0.005
Time \times site \times <i>Pisaster</i>	5	0.306	5.29	<0.01
Time \times exposure \times <i>Pisaster</i>	5	0.059	1.02	>0.25
Time \times site \times exposure \times <i>Pisaster</i>	5	0.169	2.92	>0.05
Time \times replicate (site \times exposure \times <i>Pisaster</i>)	40	0.058	1.56	<0.05
Error (time)	575	0.037		

Multivariate repeated-measures analysis (df = 5, 111 for all effects but time \times replicate (site \times exposure \times *Pisaster*), for which df = 40, 487)

Effect	Wilks' lambda	F	P
Time	0.268	60.5	0.0001
Time \times site	0.820	4.87	0.0005
Time \times exposure	0.891	2.70	0.0240
Time \times <i>Pisaster</i>	0.812	5.13	0.0003
Time \times site \times exposure	0.802	5.47	0.0002
Time \times site \times <i>Pisaster</i>	0.850	3.90	0.0027
Time \times exposure \times <i>Pisaster</i>	0.949	1.19	0.3177
Time \times site \times exposure \times <i>Pisaster</i>	0.918	1.98	0.0872
Time \times replicate (site \times exposure \times <i>Pisaster</i>)	0.588	1.58	0.0157

* Transplants ($n = 10$) nested within replicates, and replicates were treated as random effects; site, exposure, and *Pisaster* were treated as fixed. Because the design was nested, main effects and interactions were tested using the replicate(site \times exposure \times *Pisaster*) mean square as the error term. Sums of squares are Type III. Univariate tests for within-subject effects do not satisfy the Huynh-Feldt condition (do not have Type *H* covariance matrices; Test for Sphericity; $P < 0.0001$ with 14 df). Consequently, significant *F* values were obtained by adjusting the degrees of freedom (from 5, 40, and 575 to 3, 26, and 374) with the Huynh-Feldt estimator (epsilon = 0.6508) (SAS Institute 1988).

apparent within 2–4 wk (Table 3). Mortality varied with exposure throughout the experiment, and site differences in mortality persisted for 1.5 mo, when total mortality at BB exposed began to approach that at SH exposed (which was nearly 100% within a month; Fig. 9). As in 1990, mortality patterns diverged among some replicates, particularly those at SH protected (Fig. 9).

Although the data from the 1992 *M. trossulus* transplants were limited (the experiments lasted only 15 d; no data were obtained at protected sites), results were consistent with the more extensive *M. californianus* transplants. About half the mussels survived in +*Pisaster* plots at BB exposed (proportion surviving [mean \pm 1 SE]: 0.48 ± 0.05 , $n = 3$) while no mussels survived at SH exposed. Survival in –*Pisaster* plots was much

higher: 0.84 ± 0.05 at BB and 0.62 ± 0.31 at SH ($n = 3$ in both cases).

Effect of sand burial

In 1991 at SH protected, *Pisaster* did not have a significant effect on mussel mortality rates (Fig. 9). Mussels survived poorly whether or not *Pisaster* were present. The explanation of these divergent results was suggested by field observations. Transplanted mussel clumps were often partially to completely buried by sand when we made our biweekly counts. Moreover, shifting sand often re-exposed plots on subsequent visits, and dead but still attached mussels were commonly observed. Since *Pisaster* almost invariably tears mussels loose from the substratum, the persistence of at-

TABLE 3. Effects of site, exposure, and *Pisaster ochraceus* by sample date (univariate ANOVAs) in 1990 and 1991 mussel transplant experiments. See Table 2 for further explanation. Significant *F* values are in boldface.

1990 Experiment								
Source after variation	df	Sta- tistic	Days after initiation					
			12	23	39	54	67	84
			T1†	T2	T3	T4	T5	T6
Site	1	MS	3.05	1.99	0.82	0.34	0.18	0.015
		F	18.9*	4.18	1.75	1.06	0.49	0.03
Exposure	1	MS	2.76	4.04	4.19	3.32	2.80	0.94
		F	17.1*	8.49	8.92	10.28	7.44	1.66
Pisaster	1	MS	2.31	6.21	7.31	8.37	8.79	10.9
		F	14.8	13.0	15.6*	25.9**	23.3*	19.2*
Site × exposure	1	MS	1.49	0.003	0.13	0.16	0.13	0.18
		F	9.21	0.02	0.03	0.48	0.35	0.31
Site × Pisaster	1	MS	3.07	1.06	0.65	0.37	0.16	0.04
		F	19.0*	2.22	1.39	1.13	0.42	0.06
Exposure × Pisaster	1	MS	1.93	2.47	2.77	2.63	2.24	1.01
		F	11.9	5.18	5.91	8.16	5.95	1.77
Site × exposure × Pisaster	1	MS	2.53	0.84	0.61	0.29	0.23	0.39
		F	15.7*	1.77	1.30	0.89	0.60	0.68
Replicate (site × exposure × Pisaster)	8	MS	0.16	0.48	0.47	0.32	0.38	0.57
		F	2.59	3.92**	3.86**	2.69*	3.39**	5.67**
Overall model	15	MS	1.62	1.65	1.59	1.40	1.33	1.28
		F	25.9***	13.5***	13.1***	11.7***	12.0***	12.7***
Error	115	MS	0.063	0.121	0.122	0.120	0.111	0.100
R ²			0.772	0.639	0.630	0.604	0.610	0.624

1991 Experiment								
Source of variation	df	Sta- tistic	Days after initiation					
			Boiler Bay: Strawberry Hill:	16 12	31 28	46 43	59 59	75 72
			T1	T2	T3	T4	T5	
Site	1	MS	3.20	4.60	3.73	2.12	1.50	
		F	11.8*	23.3*	18.5*	8.36	5.91	
Exposure	1	MS	0.52	0.50	0.45	0.37	0.15	
		F	1.93	2.53	2.23	1.45	0.86	
Pisaster	1	MS	3.40	6.60	7.81	10.6	12.7	
		F	12.6*	33.4**	38.8**	41.7***	75.8***	
Site × exposure	1	MS	0.02	0.07	0.18	0.45	1.01	
		F	0.06	0.37	0.87	1.78	6.04	
Site × Pisaster	1	MS	0.96	2.62	2.19	0.99	0.62	
		F	3.53	13.3*	10.9	3.92	3.71	
Exposure × Pisaster	1	MS	1.36	3.09	3.60	3.96	3.68	
		F	5.00	15.6*	17.9*	15.6*	21.9*	
Site × exposure × Pisaster	1	MS	0.92	1.04	0.94	0.82	0.62	
		F	3.39	5.25	4.70	3.23	3.70	
Replicate (site × exposure × Pisaster)	8	MS	0.27	0.20	0.20	0.25	0.17	
		F	2.59	2.03	2.11	2.21	1.54	
Overall model	15	MS	1.01	1.65	1.68	1.71	1.73	
		F	9.6***	16.9***	17.6***	15.0***	15.8***	
Error	119	MS	0.104	0.097	0.095	0.114	0.109	
R ²			0.548	0.681	0.689	0.654	0.666	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ (ANOVA *F*). Significance levels were adjusted with the Bonferroni approximation, giving $P < 0.0083$ (1990) and $P < 0.01$ (1991) for the overall 5% level of significance. Data are Type III mean squares (MS) and *F* values.

† T1 to T6 indicate sample times.

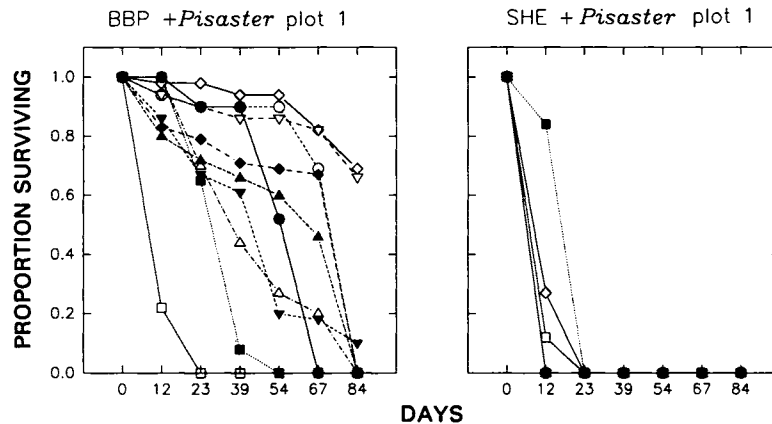


FIG. 8. Survival curves for each of 10 individual transplant clumps in +*Pisaster* treatments in large plot 1 at Boiler Bay protected and large plot 1 at Strawberry Hill exposed. At Strawberry Hill, survival in 7 of the 10 clumps in the plot after 12 d was zero.

tachment in these mussels suggests some other factor caused mortality. In some cases, we were able to relocate buried mussels by digging or pouring buckets of water over them. Uncovered mussels included both living and dead individuals, the latter of which were

rotting in situ. Hence, in both years, but especially 1991, mussels at SH protected suffered mortality from burial by sand; predation by seastars or other predators seemed a lesser source of mortality.

To evaluate the survival of mussels buried by sand, we examined mussel survival after different times of burial. Burial duration was estimated as the number of days between the first and last date of burial. For example, if a clump was buried after 12, 28, and 43 d but not at 59 d, we estimated the burial duration as $43 - 12 = 31$ d.

While partial burial was often associated with reduced survival, survival of mussels partly buried did not vary through time (Fig. 10; linear regression for both years combined; $F = 1.16$, 1, 56 df, $P = 0.29$, $R^2 = 0.003$). Survival of totally buried mussels declined sharply through time, however (linear regression for both years combined; $F = 8.53$, 1, 33 df, $P = 0.006$, $R^2 = 0.18$). *M. californianus* appears able to survive sand burial no longer than ≈ 2 mo (Fig. 10). In fact, survival time may be much shorter. In several plots, all mussels had died within 12–18 d (Fig. 10). Since we could not be present constantly, it is possible that those mussels surviving “total” burial periods >10–20 d were in fact not buried constantly, but due to shifting sand, underwent periods of total and partial burial. Hence, although the actual period of tolerance of burial by *M. californianus* is somewhat uncertain, sand burial can evidently be an important source of mortality of mussels in the low zone at SH protected.

These results do not eliminate an alternative cause of low mussel survival at SH low protected, i.e., the presence of crabs or other predators. To test this possibility, we examined mussel survival data from the caged mussel transplant study (Fig. 11). Survival of these mussels, all of which were caged continuously for 12 mo (June 1991–June 1992) and therefore were largely free of mortality from predators, was high in both mid and low zones at all locations \times exposures except

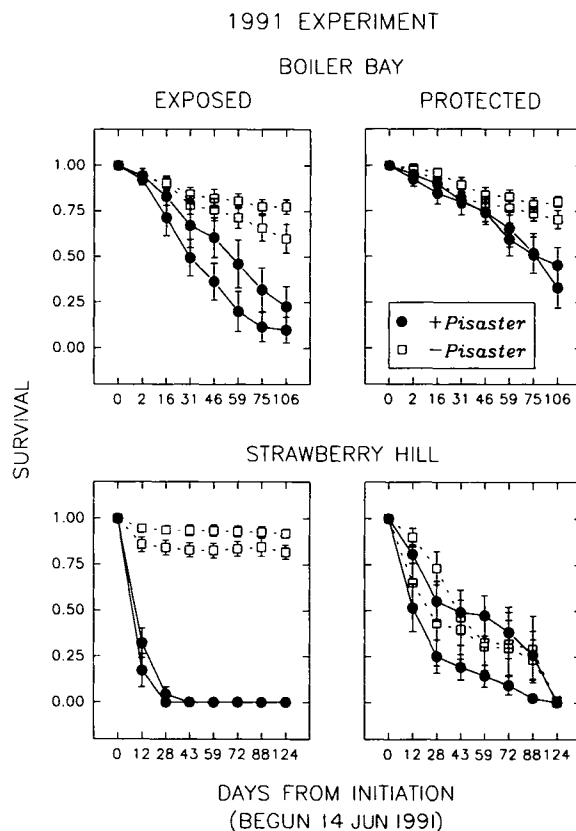


FIG. 9. Results of 1991 mussel transplant experiment (means ± 1 SE). Sample days (horizontal axes) differed between Boiler Bay and Strawberry Hill. See caption of Fig. 5 for further explanation.

TABLE 4. Repeated-measures analysis of variance (nested) of the effect of site, exposure, and seastar predation on mussel survival after 12/16, 28/31, 43/46, 59, 72/75, and 88/106 days (see Fig. 9) in summer 1991.*

Source of variation	df	MS	F	P
Between subjects				
Site	1	14.6	35.9	<0.0001
Exposure	1	1.91	4.69	0.032
<i>Pisaster</i>	1	39.3	96.8	<0.0001
Site \times exposure	1	1.00	2.47	0.12
Site \times <i>Pisaster</i>	1	6.88	16.9	<0.0001
Exposure \times <i>Pisaster</i>	1	15.2	37.5	<0.0001
Site \times exposure \times <i>Pisaster</i>	1	4.31	10.6	0.0015
Replicate (site \times exposure \times <i>Pisaster</i>)	8	0.984	2.42	0.019
Error	119	0.406		
Within subjects				
Time	5	4.03	89.4	<0.0001
Time \times site	5	0.182	4.04	<0.025
Time \times exposure	5	0.026	0.58	>0.50
Time \times <i>Pisaster</i>	5	0.586	13.0	<0.0001
Time \times site \times exposure	5	0.241	5.35	<0.01
Time \times site \times <i>Pisaster</i>	5	0.170	3.77	<0.05
Time \times exposure \times <i>Pisaster</i>	5	0.150	3.33	<0.05
Time \times site \times exposure \times <i>Pisaster</i>	5	0.010	0.23	>0.75
Time \times replicate (site \times exposure \times <i>Pisaster</i>)	32	0.045	0.96	>0.25
Error (time)	476	0.047		

Multivariate repeated-measures analysis (df = 4, 116 for all effects but time \times replicate (site \times exposure \times *Pisaster*), for which df = 32, 429)

Effect	Wilks' lambda	F	P
Time	0.380	47.2	0.0001
Time \times site	0.890	3.59	0.0085
Time \times exposure	0.979	0.62	0.65
Time \times <i>Pisaster</i>	0.820	6.37	0.0001
Time \times site \times exposure	0.903	3.10	0.018
Time \times site \times <i>Pisaster</i>	0.868	4.40	0.002
Time \times exposure \times <i>Pisaster</i>	0.937	1.95	0.11
Time \times site \times exposure \times <i>Pisaster</i>	0.992	0.22	0.93
Time \times replicate (site \times exposure \times <i>Pisaster</i>)	0.851	0.60	0.96

* Univariate within subjects *F* values were obtained by adjusting the degrees of freedom (from 5, 32, and 476 to 3, 19, and 289) with the Huynh-Feldt estimator (epsilon = 0.6081). See Table 2 caption for further detail.

SH low protected (Fig. 11; Table 5). Thus, in the absence of large predators (seastars, crabs, birds, fishes), mussels survived well except at the site where sand burial was a regular annual event. Whelks, which were not excluded by cages, are not likely to be the cause of the low survival at SH low protected, both because whelks were found in all cages at all sites and because the mussels were too large to be eaten by whelks. These considerations suggest that mortality of mussels at this site depended on sand burial, which occurred independently of the presence or absence of predators/cages.

Effectiveness of Pisaster removal

As mentioned above, in both 1990 and 1991 mussel transplant experiments, some mussel mortality occurred in $-Pisaster$ plots. Most of this mortality appeared due to seastars evading removal efforts and not to other predators such as crabs, birds, whelks, or fishes. First, most mussels in these experiments were either too large or too firmly attached for most birds, whelks,

or fishes to be able to remove and consume them. Moreover, although Dittman and Robles (1991) and Wootton (1993) observed oystercatchers eating California mussels, these birds were judged to be minor sources of mortality. Our observations in Oregon are consistent with those of these investigators. Second, we never found crushed California mussel shells such as those crabs would leave in or near the transplants. Third, none of these predators except whelks appeared common at our sites, although observations were not made at high tide due to the usually turbulent conditions. Fourth, as detailed below, seastars were commonly found actually feeding on mussel clumps in $-Pisaster$ plots.

As documented in the Appendix (and observed by Paine [1974] in his experiments), manual removal of seastars results in a reduction and not an elimination of seastar predation. For example, on average, between 12.1 and 38.4% of the original number removed were found to have reinvaded $-Pisaster$ plots on our regular removal visits (Appendix). While these data suggest

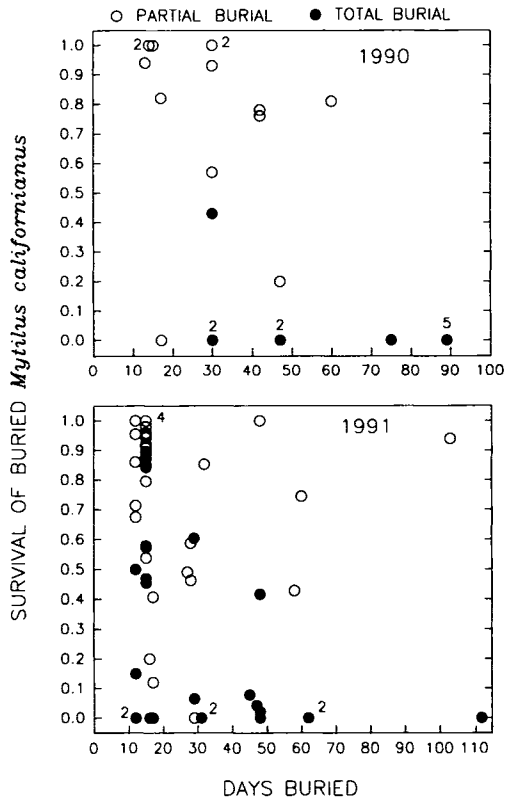


FIG. 10. Survival of *Mytilus californianus* totally or partially buried by sand for varying time periods in the 1990 and 1991 experiments at Strawberry Hill protected. Numbers by a symbol indicate that more than one observation occurred for that point.

our efforts were effective, reinvasion by *Pisaster* was sometimes relatively rapid, especially in the warmer months of the year. A further indication of the effectiveness of removal efforts is suggested in Table 6. These data reflect the general patterns of predation intensity summarized earlier (Tables 2–4; Figs. 7 and 9), but also indicate that efforts to protect transplant clumps from *Pisaster* were more successful in 1991 than in 1990. In seven of eight cases, mean percent of total clump-sample dates with *Pisaster* present in removal plots were lower in 1991 than in 1990 (Table 6). This greater success probably reflected increased efficiency in locating invading seastars and improved location of clumps. A few were placed slightly higher on the shore, while others were placed farther away from favored seastar invasion routes (e.g., certain crevices or channels). These changes led to a particularly dramatic improvement at SH exposed (from 68 and 51.4% of plots located by seastars in 1990 to 4.3 and 4.3% located in 1991). Overall, the relatively high survival of mussels in 1991 seastar removal plots further supports the notion that predators other than *Pisaster* were not the cause of mussel mortality in 1990 seastar removal plots.

Effect of turf on mussel survival

In 1990, mussel survival did not differ in the presence and absence of an algal turf (split-plot ANOVA for each date at each site \times exposure combination; *Pisaster* and turf were considered between- and within-plot treatments, respectively; $P \gg 0.05$ in all cases, 1, 2 df). Although low replication weakens the power of these tests, no trends were apparent to suggest repetition of this experiment. These data and observations indicate that turf had little effect on mussel survival either through an influence on firmness of attachment or by hindering seastar feeding on partially hidden mussels. This experiment did not involve removal of turf around the clump, however, so no conclusions regarding the effect of algal turf on foraging activity are possible.

Effect of predation: prey and community responses

Removal of seastars had a large effect on sessile prey abundance at SH exposed (Fig. 12), but no effect at either SH protected or BB (data not shown). At SH exposed, mussel (*M. trossulus*) abundance generally increased from June 1990 through May 1991 (Fig. 12).

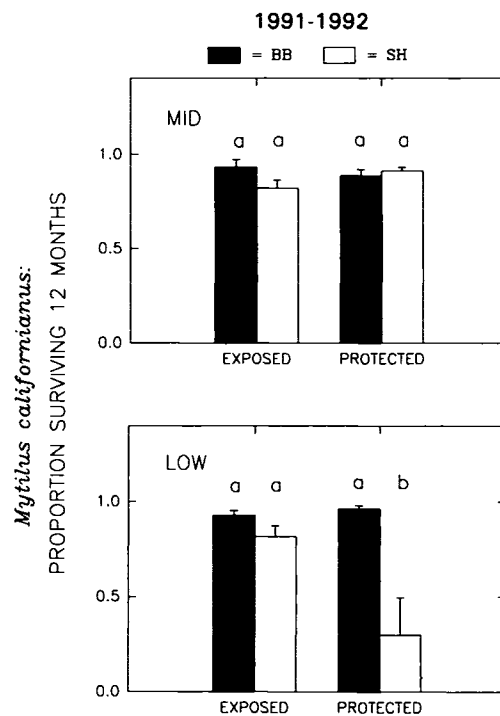


FIG. 11. Survival of transplanted caged *M. californianus* after 12 mo (means \pm 1 SE). Bars with different lowercase letters indicate means are significantly different. Five clumps of 30 marked individuals each were transplanted to the low zone at each site \times exposure combination. All mussels were from the same source, Seal Rock (located between Strawberry Hill and Boiler Bay).

TABLE 5. Three-way ANOVA on the 1-yr survival of marked *Mytilus californianus* transplanted to cages in mid and low intertidal zones at exposed and protected sites at Boiler Bay and Strawberry Hill.*

Source of variation	df	MS	F	P
Location (BB vs. SH)	1	1.062	14.5	0.0006
Wave exposure (exposed vs. protected)	1	0.206	2.82	0.1
Tidal level (mid vs. low)	1	0.345	4.72	0.038
Location \times wave exposure	1	0.177	2.42	0.13
Location \times tidal level	1	0.479	6.54	0.016
Wave exposure \times tidal level	1	0.239	3.26	0.08
Location \times wave exposure \times tidal level	1	0.642	8.77	0.006
Error	30	0.073		

* Since mussel clumps ($n = 5$ in each location \times exposure \times level combination) were established haphazardly in each zone at each site (i.e., were not nested within another treatment), each clump of 30 mussels was considered a replicate.

Algal turf had no effect on mussel abundance, and no seastar effect was observed until August 1991 (Fig. 12, Table 7; time \times *Pisaster* effect was significant). *Pisaster* foraging activity declines in winter and increases in spring (B. A. Menge et al., *personal observations*; see also Mauzey et al. 1968, Menge 1972, Paine 1974), indicating the buildup in mussel cover occurred while seastars were relatively inactive. The sharp drop in mussel cover in +*Pisaster* plots over the summer (Fig. 12) coincided with peak seastar foraging activity.

Over the longer term, as at Paine's sites in Washington (Paine 1966, 1974, 1984), *Mytilus californianus* at wave-exposed sites migrated downward into the low zone in -*Pisaster* plots. By March 1993, at SH exposed, the lower edge of the mussel bed at the two -*Pisaster* plots had moved 1.94 ± 0.9 m (mean \pm 1 SD, $n = 10$ measurements) and 1.02 ± 0.5 m ($n = 13$). These distances represented mean vertical drops of 0.47 ± 0.02 and 0.63 ± 0.07 m, respectively. At BB exposed, the approximate distance moved at one site was 0.83 ± 0.3 m ($n = 5$), representing a vertical drop of ≈ 0.3 m. Although a large chunk of the mussel bed on the second BB exposed area disappeared with its underlying substratum in winter 1993, measurements of the remnant suggested the lower limit of this mussel bed had also dropped ≈ 0.4 m. No change was observed in the lower limit of the mussel bed in any +*Pisaster* exposed large plot or at any sheltered site regardless of *Pisaster* treatment. In comparison, Paine (1974) measured advances of the lower edge of the mussel bed at Tatoosh Island from 1970–1973 of 1.93 ± 0.5 (-*Pisaster*) and 0.1 ± 0.07 m (+*Pisaster*). Hence, mussel bed dynamics at exposed sites in Oregon were similar to those in Washington (Paine 1974, 1984); the mussels respond to diminished predation at their lower edge by pushing and being pushed by their neighbors into lower portions of the shore.

These results raise two questions. First, why did mussel abundance (both species) increase at exposed sites, especially SH, but not at protected sites? Second, why didn't *M. trossulus* continue to increase in abundance (rather than level off, as observed) in -*Pisaster* plots at SH exposed (Fig. 12)? These questions are considered in turn below.

Mussel recruitment

Recruitment density of mussels, probably primarily *M. trossulus*, was higher at wave-exposed than wave-protected sites, and higher at SH than at BB (Fig. 13). Recruitment patterns were similar in mid and low zones (Fig. 13). From 1989–1992, mussel recruitment generally occurred between June and December each year. Peak recruitment was higher in 1989 and 1990 than

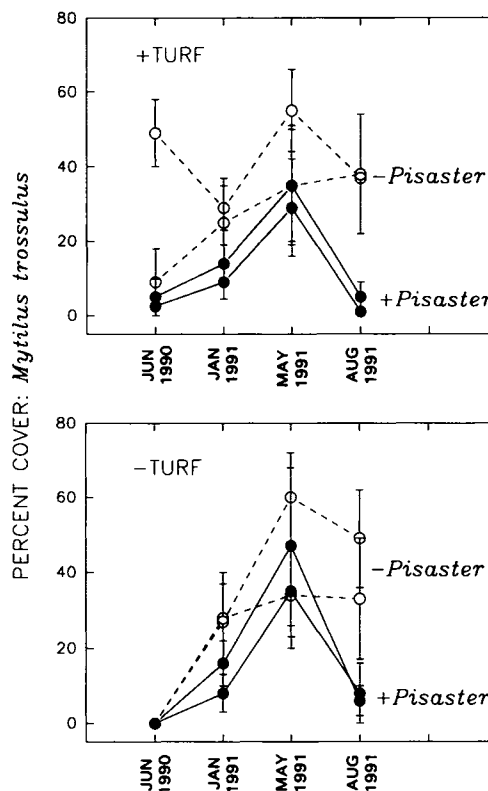


FIG. 12. Changes in abundance of the mussel *Mytilus trossulus* under experimental conditions in 20×20 cm marked quadrats at Strawberry Hill exposed. +TURF and -TURF, and +*Pisaster* and -*Pisaster* indicate presence and absence of an algal turf and *Pisaster*, respectively. Data are mean \pm 1 standard error ($n = 5$ marked plots) for each turf \times *Pisaster* treatment combination. The experiments were begun in June 1990 and sampled in January, May, and August 1991.

TABLE 6. Number of mussel transplant clumps (of 10 per site) located by *Pisaster ochraceus* in 1990 and 1991 experiments. Site code: SH = Strawberry Hill; BB = Boiler Bay; E = exposed; P = protected; +P = *Pisaster* present; -P = *Pisaster* removed; 1 = replicate plot 1; 2 = replicate plot 2. Dates \times clumps = 60 with six sample dates, 70 with seven dates.

Site code	1990 1991	Sample date							% of clump- dates with <i>Pisaster</i>
		Jun 24 Jun 27	Jul 6 Jul 11	Jul 21 Jul 26	Aug 6 Aug 10	Aug 19 Aug 23	Sep 5 Sep 8	Sep 19 Oct 9	
BBE +P1	1990	1	6	6	9	9	9	...	66.7
	1991	0	1	4	5	6	7	10	47.1
BBE +P2	1990	1	7	9	10	10	10	...	78.3
	1991	1	2	4	8	9	9	9	60.0
BBE +P totals		3	16	23	32	34	35	...	59.6
BBE -P1	1990	3	6	6	6	6	8	...	58.3
	1991	0	0	1	2	2	2	4	16.7
BBE -P2	1990	0	2	2	4	6	7	...	35.0
	1991	0	2	2	2	4	5	6	30.0
BBE -P totals		3	10	11	14	18	22	...	32.5
BBP +P1	1990	0	1	2	2	4	5	...	23.3
	1991	1	1	2	4	4	5	8	35.7
BBP +P2	1990	1	4	4	6	6	8	...	48.3
	1991	0	0	0	3	6	7	7	32.9
BBP +P totals		2	6	8	15	20	25	...	31.7
BBP -P1	1990	0	0	1	3	3	6	...	21.7
	1991	0	0	2	2	3	3	5	21.4
BBP -P2	1990	0	0	0	1	1	2	...	6.7
	1991	0	0	0	0	0	1	3	5.7
BBP -P totals		0	0	3	6	7	12	...	11.7
SHE +P1	1990	10	10	10	10	10	10	10	100.0
	1991	9	10	10	10	10	10	10	98.6
SHE +P2	1990	10	10	10	10	10	10	10	100.0
	1991	10	10	10	10	10	10	10	100.0
SHE +P totals		39	40	40	40	40	40	40	99.6
SHE -P1	1990	1	8	8	8	9	68.0
	1991	0	0	0	0	1	1	1	4.3
SHE -P2	1990	2	5	5	5	6	6	7	51.4
	1991	0	0	0	0	1	1	1	4.3
SHE -P totals		3	13	13	13	17	29.5
SHP +P1	1990	0	0	2	2	2	5	5	22.9
	1991	1	2	2	2	2	2	2	18.6
SHP +P2	1990	2	7	8	8	9	10	10	77.1
	1991	1	1	1	1	1	1	1	10.0
SHP +P totals		4	10	13	13	14	18	18	32.1
SHP -P1	1990	1	2	2	2	2	2	2	18.6
	1991	1	1	1	1	1	1	1	10.0
SHP -P2	1990	0	0	0	0	0	0	0	0.0
	1991	4	5	5	5	5	5	5	48.6
SHP -P totals		6	8	8	8	8	8	8	19.3

in 1991 and 1992. The patterns in Fig. 13 suggest the 1990–1991 mussel buildup at SH exposed (Fig. 12) was a result of dense recruitment, while the lack of change in abundance of mussels at any other site during the same time was due to low recruitment (note the differences in scale of the ordinates). This site- and exposure-related recruitment pattern appeared consistent through time, since it occurred in all four years (1989–1992) despite temporal variation. Thus, low recruitment may be another factor contributing to the general scarcity of mussels in the low zone at three of the four site \times exposure combinations.

Field observations were consistent with these patterns. Every winter since 1989, dense beds of *M. trosulus* developed in the low zone at SH exposed but at no other site. After a time lag of 2–3 mo, these mussels first became noticeable at 3–5 mm shell length in late autumn and aggregated most densely in crevices and among barnacles. Modal size clearly increased through winter, until mussels of 4–5 cm were dominant.

Mussel growth

In both 1990–1991 and 1991–1992, growth of *M. californianus* varied with site and exposure (Fig. 14;

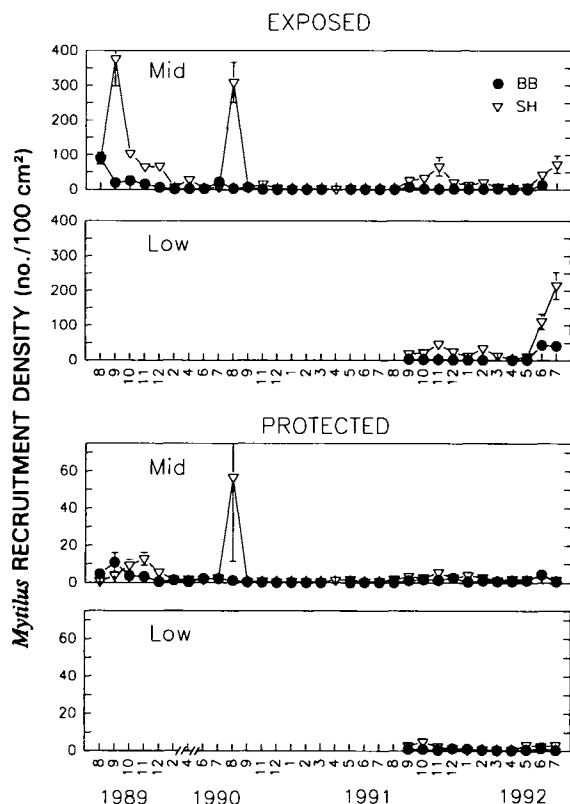


FIG. 13. Recruitment densities of mussels attached to artificial collectors (see *Methods: Experimental design: Mussel recruitment*) in the mid and low intertidal zones of Boiler Bay and Strawberry Hill exposed and protected sites. Data are number of mussels ≤ 1 mm in shell length (means ± 1 SE; $n = 5$ collectors per month). Note the scale differences in the ordinates for exposed vs. protected panels.

Table 8). Mussels at SH grew approximately twice as much as those at BB and twice (1991) to half again as much (1990) at exposed than at protected locations (Fig. 14). The absence of a significant site \times exposure interaction (Table 8) suggests that the conditions leading to faster growth at SH were uniformly better at both wave exposures, and that the degree to which conditions for growth were favorable decreased uniformly with decreased wave force. Since these sessile invertebrates feed on particles filtered from the water, these differences in growth suggest that detritus and/or phytoplankton abundance is higher at SH and higher at exposed than at protected sites. These results also suggest that per-individual rates of secondary production of mussel tissue is greater at SH and at wave-exposed locations.

Response of Nucella spp. to Pisaster manipulation

Why didn't *M. trossulus* continue increasing in abundance in marked plots at SH exposed in the absence of *Pisaster*? Field observations in spring 1991 indicated

that in $-Pisaster$ plots, whelks, primarily *Nucella canaliculata* but also *N. emarginata*, had increased dramatically in abundance. No such changes were evident in $+Pisaster$ plots. Moreover, *N. canaliculata* shell length (but not *N. emarginata* length) also appeared much greater in $-Pisaster$ than in $+Pisaster$ plots.

Estimates of whelk densities confirmed these impressions (Fig. 15). When experiments were begun in June 1990, *Nucella* spp. were generally scarce at all site \times exposure combinations (Fig. 15, open bars), and in June 1991 were still scarce at BB (Fig. 15, top panels; note the differences in scales of the ordinates). At SH exposed, however, abundances of both whelks in $-Pisaster$ plots had greatly increased by June 1991, while changes in $+Pisaster$ plots were relatively slight (Fig. 15). Mean numbers of *N. canaliculata*/0.25 m², for instance, increased by 1.3 and 4.1 snails in $+Pisaster$ plots and 29.2 and 22.1 snails in $-Pisaster$ plots. Comparable changes in *N. emarginata* were 0.2 and -0.4 snails ($+Pisaster$) vs. 14.7 and 3.8 snails ($-Pisaster$). Although variances were too heteroscedastic to justify

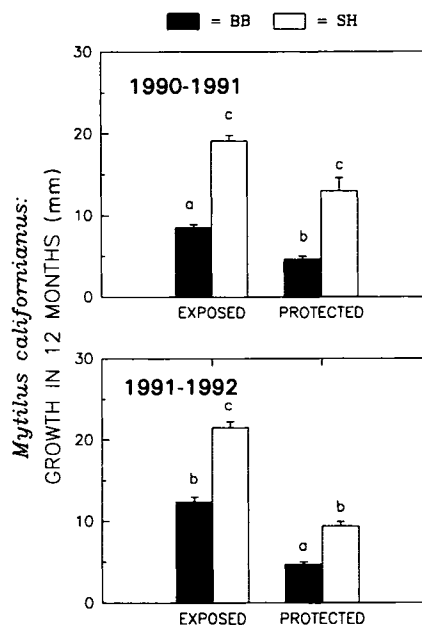


FIG. 14. Growth (mean and 1SE) of transplanted mussels at each site \times exposure combination. Bars with different lowercase letters are significantly different (see Table 8). 1990–1991 data were reported in Menge 1992 and are included here for comparison to 1991–1992 data. 1990–1991 data were from mussels surviving the 1990 transplant experiments, so sample sizes varied: BBE, 129 mussels; BBP, 17; SHE, 139; SHP, 10. 1991–1992 data were from survivors in clumps of transplanted, caged mussels ($n = 5$ cages of 30 individuals each per site \times exposure combination, see Fig. 11 for survival data). Sample sizes (total live mussels per site \times exposure combination) were BBE, 89; BBP, 115; SHE, 99; SHP, 66. Mussel sources in 1990–1991 were mid-zone mussel beds at each site. To avoid the possibility that growth reflected site-related genetic differences, 1991–1992 mussels were all obtained from Seal Rock, located between SH and BB.

TABLE 7. Repeated-measures analysis of variance of the effect of seastar predation and turf (split-plot design) on abundance of the mussel *Mytilus trossulus* in marked quadrats at the wave-exposed site at Strawberry Hill in January, May, and August 1991.*

Source of variation	df	MS	F	P
Between subjects (treatment effects averaged over time)				
<i>Pisaster</i>	1	2.86	6.81	>0.1
Turf	1	0.041	3.42	>0.1
<i>Pisaster</i> × turf	1	0.010	0.83	>0.25
Plot(<i>Pisaster</i>)	2	0.420	1.51	0.23
Turf × plot(<i>Pisaster</i>)	2	0.012	0.04	0.96
Error	40	0.278		
Within subjects (time effects)				
Time	2	1.058	12.54	<0.0001
Time × <i>Pisaster</i>	2	0.435	8.37	<0.05
Time × turf	2	0.011	1.10	>0.25
Time × <i>Pisaster</i> × turf	2	0.009	0.90	>0.25
Time × plot(<i>Pisaster</i>)	4	0.052	0.620	0.65
Time × turf × plot(<i>Pisaster</i>)	4	0.010	0.121	0.98
Error	80	0.084		

Multivariate repeated-measures analysis [df = 2, 39 for all effects but time × plot(*Pisaster*) and time × turf × plot(*Pisaster*), for which df = 4, 78].

Effect	Wilks' lambda	F	P
Time	0.642	10.89	<0.0001
Time × <i>Pisaster</i>	0.814	4.46	0.018
Time × turf	0.992	0.158	0.854
Time × <i>Pisaster</i> × turf	0.993	0.133	0.876
Time × plot(<i>Pisaster</i>)	0.933	0.693	0.599
Time × turf × plot(<i>Pisaster</i>)	0.986	0.135	0.969

* *Pisaster* and turf treatments were considered fixed and plots were considered random. Sums of squares are Type III. Univariate tests for within-subject effects satisfied the Huynh-Feldt condition, so standard *F* values were used. Because marked quadrats were nested within *Pisaster* plots, *Pisaster* effects were tested using plot(*Pisaster*) as the error term, and turf and the *Pisaster* × turf interaction were tested using turf × plot(*Pisaster*) as the error term.

TABLE 8. Effect of site (Boiler Bay vs. Strawberry Hill) and exposure (wave-exposed vs. wave-protected) on growth rates of transplanted *Mytilus californianus* (two-way ANOVA)*. In 1990, mussels were transplanted from the mid to the low intertidal zone at each site. In 1991, mussels were transplanted from a common mid zone source (Seal Rock, located between sites) to the low zones of each site.

Analysis	Source of variation	df	MS	F	P	% variance explained	Variance homogeneity (Cochran's C)	Unplanned comparisons	
								Test†	Order
1990	Site	1	17.19	72.3	<.0001	19.1			
	Exposure	1	3.48	14.6	.0002	3.9			
	Site × exposure	1	0.02	0.08	.784	0.02			
						Σ = 23.0	P < 0.05	GH	BBP < BBE < SHP = SHE
	Error	291	0.238						
	Total	294							
1991	Site	1	1.63	15.3	.0012	26.2			
	Exposure	1	2.87	26.9	.0001	46.2			
	Site × exposure	1	0.004	0.04	.854	0.06			
						Σ = 72.5	P > 0.05	RQ	BBP < SHP = BBE < SHE
	Error	16	0.107						
	Total	19							

* In all analyses, outliers were eliminated until normality and independence of errors were evident in probability plots of residuals and plots of residuals × estimates, respectively. In 1990, mussels sampled were those surviving predation in uncaged mussel transplant experiments in the four large plots at each site × exposure combination, so individuals were treated as replicates. In 1991, transplanted mussels (30 individuals in each of five clumps) were caged to protect them from predation. Preliminary analyses (ANCOVA, with initial length as covariate) indicated significant between-cage differences, so mean per-capita growth increments were used as replicates. 1990 data were presented previously (Menge 1992); they are included here and analyzed for comparison with the 1991 data.

† Unplanned comparisons tests (Day and Quinn 1989): GH, Games and Howell method (unequal variances, unequal samples); RQ, Ryan's *Q* test.

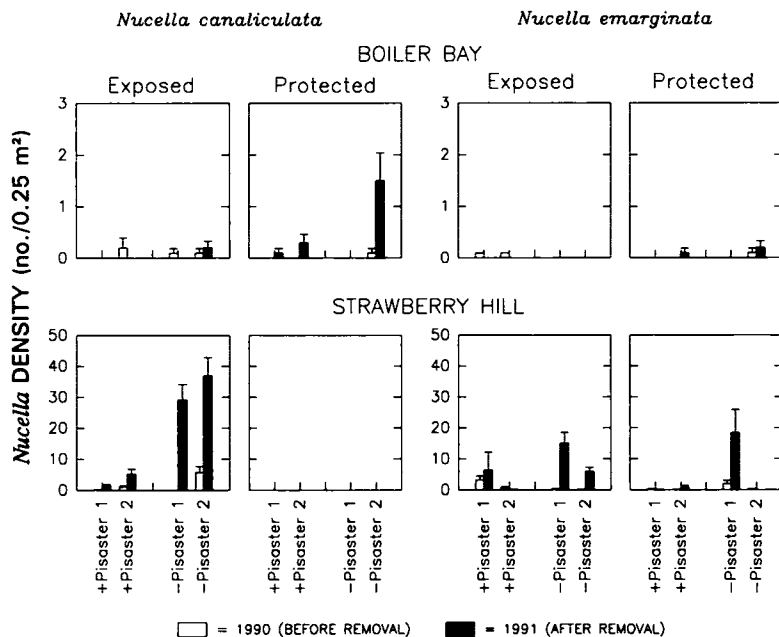


FIG. 15. Density of the whelks *Nucella canaliculata* and *N. emarginata* in the presence and absence of *Pisaster* before and 12 mo after seastar removals at each site \times exposure combination. Data are mean \pm 1 standard error per 0.25 m² ($n = 15$ quadrats sampled before and 10 quadrats sampled 12 mo after *Pisaster* removal). Note the scale differences in ordinates at Boiler Bay vs. Strawberry Hill.

use of ANOVA, examination of both the magnitude of change and the error bars (= standard errors) in Fig. 15 suggests the increases from 1990 to 1991 in the absence of *Pisaster* were ecologically significant, while those in the presence of *Pisaster* were not. At SH protected, no comparable changes occurred with the exception of one $-$ *Pisaster* plot in which *N. emarginata* increased from 1.9 to 18.4 snails/0.25 m² from 1990 to 1991.

At SH exposed, the removal of *Pisaster* evidently led to a dramatic shift in size structure of *N. canaliculata* as well (Fig. 16). Mean shell length after 12 mo of seastar removal (June 1991) was 3–7.6 mm longer in whelk populations from $-$ *Pisaster* plots than in $+$ *Pisaster* plots, with no overlap in 95% confidence intervals between seastar treatments (confidence intervals: $-$ *Pisaster*, 21.4–23.0 mm and 18.1–19.7 mm; $+$ *Pisaster*, 15.1–16.7 mm and 13.8–15.4 mm). Despite this trend, however, the statistical test lacked power due to low degrees of freedom (assuming large plots were replicates with whelk populations nested within plots; one-way nested ANOVA, $F = 10.95$, 1, 2 df, $P > 0.05$). Although we did not quantify size structure in 1990, observations at nearby wave-exposed nonexperimental sites indicated that sizes in $+$ *Pisaster* plots were generally representative of the area. Shell lengths at all other sites \times exposures appeared unchanged (B. A. Menge et al., *personal observations*).

These data suggest *M. trossulus* abundance stopped increasing in $-$ *Pisaster* plots at SH exposed (Fig. 12)

because whelks, also predators of mussels and barnacles (Connell 1970, Dayton 1971), had increased in size and abundance and thereby increased the intensity of their predation. This interpretation needs experimental confirmation, but whelks preyed heavily on *M. trossulus*, and often mussels were considerably larger than the whelks feeding on them (B. A. Menge et al., *personal observations*). We also observed that *Nucella* were laying higher densities of egg capsules in $-$ *Pisaster* plots than in $+$ *Pisaster* plots, suggesting high whelk densities were likely to persist.

DISCUSSION

We emphasize three major points. First, as in Washington, *Pisaster ochraceus* was a keystone predator at our wave-exposed sites. However, while perhaps occurring broadly, especially at wave-exposed headlands, this effect does not seem universal (e.g., this paper, Paine 1980, Robles 1987, Foster 1990, Robles and Robb 1993). Second, insight into some causes of this variation in keystone predation were obtained by performing experiments spanning several scales in space and time, and by investigating other factors such as mussel recruitment, sand burial, algal turf, and the responses of whelks. Third, keystone predation is evidently but one of several predation models. Predation can be weak, where stress or low productivity prevent significant predator impacts, to keystone, or single-species control, to diffuse, or multispecies control.

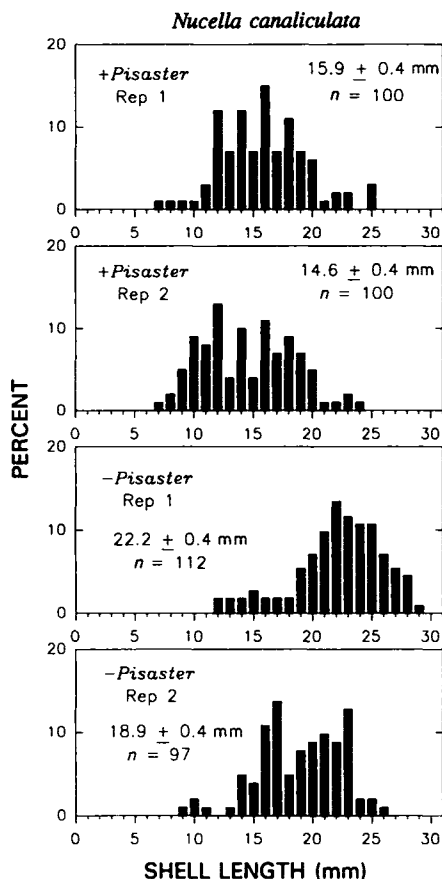


FIG. 16. Size structure (shell length) of *Nucella canaliculata* at Strawberry Hill exposed in each large plot (Rep 1 and Rep 2) in +*Pisaster* and -*Pisaster* treatments 12 mo after seastar removal was initiated. Mean ± 1 standard error and sample size are shown in each panel.

Keystone predation

Effect of *Pisaster* at wave-exposed sites.—At wave-exposed sites, survival of mussels in the absence of *Pisaster* was relatively high (Figs. 7 and 9), as was survival of caged mussels (i.e., in the absence of all predators; Fig. 11). Although our methods of predator manipulation and experiment duration differed, *Pisaster* was responsible for most mortality of transplanted *M. californianus*, indicating the seastar was a keystone predator. Moreover, this seastar served a similar role at all four wave-exposed sites tested (two Oregon sites, two Washington sites [see Paine 1974]). More generally, observations elsewhere (15 wave-exposed headlands on Vancouver Island, Washington, Oregon, central California, Santa Cruz Island, and Baja California; B. A. Menge, *personal observations*) revealed broadly similar patterns at many wave-exposed headlands, suggesting a similarly strong interaction between *Pisaster* and *M. californianus*. If so, *Pisaster* may frequently serve as a keystone predator on wave-exposed headlands along much of the west coast of North America, as concluded earlier by Paine (1969).

Role of whelks at SH exposed.—For *Pisaster* to be a keystone predator, other predators must have minimal effects. Their abundance and earlier work (e.g., Connell 1970, Dayton 1971) suggests whelks may be important predators. Further, at SH exposed, whelk populations evidently checked increases in *M. trossulus* abundance (Figs. 12, 15, and 16), suggesting *Nucella* spp. can compensate for reductions in other predators. While this does not necessarily imply whelks are keystone or even important predators under normal conditions, further consideration seems warranted.

The probable mechanism of the changes implies a weak community effect of whelks at SH exposed. *Nucella* could have increased either because of a reduction in predation by *Pisaster* (a direct effect), because of an increase in prey abundance upon a release from exploitation competition (an indirect effect), or both. Field observations support the prey increase hypothesis. Seastar abundance was manipulated at all site \times wave exposure combinations, while changes in prey abundance occurred only at SH exposed. If predation by seastars was the basis of changes in whelk populations, then such changes should have been apparent in all -*Pisaster* plots. If an increase in prey abundance underlaid the changes, then whelks would be expected to increase only in those plots with increased prey, as was observed. Nonetheless, either alternative would suggest strong whelk effects depend on reductions in seastars, implying that whelks are normally relatively unimportant in controlling low zone community structure.

Several additional considerations also suggest whelk predation is unlikely ever to be as effective at wave-exposed sites as seastar predation. Most importantly, while they may stem increases in *M. trossulus*, whelks appear ineffective in controlling *M. californianus* because these mussels can grow to invulnerable sizes (e.g., Paine 1976) and whelks are much smaller than seastars. In linear dimensions, whelks are approximately one order of magnitude smaller (≈ 2 cm in shell length vs. 20 cm in seastar diameter). In biomass, whelks are nearly two orders of magnitude smaller (≈ 3 g wet mass vs. ≈ 200 g wet mass for seastars). Thus, in both our seastar removal experiments and those of Paine (1966, 1974), California mussels moved down the shore despite the presence of whelk populations, which, in Oregon at least, were more abundant than usual and consisted of larger individuals (Figs. 15 and 16).

Compared to seastars, whelk numerical, functional, and developmental responses make them ill-suited as potential keystone predators. For instance, small size, low mobility, low dispersal ability, and a patchy dispersion combined underlie weak numerical response capability. *Nucella* spp. were scarce in the low zone at BB, and at BB exposed, were distributed randomly (Figs. 15 and 17; data fit a Poisson distribution, $\chi^2 = 0.47$, $P > 0.1$; whelks were too rare at BB protected to test dispersion). At SH, *Nucella* were more abundant (Figs. 15 and 17), but were distributed patchily over

the substratum (Fig. 17; 10 of 40 quadrats had >10 individuals; dispersion is nonrandom, $\chi^2 = 149.8$, $P \ll 0.001$). Whelks are thus either scarce, or when abundant, relatively contagiously dispersed. Because they are smaller, and never grow to sizes remotely approaching those of seastars (thus having a relatively weak developmental response; Murdoch 1971), whelk mobility is low relative to that of seastars. Moreover, the potential functional response of these predatory gastropods, which can eat prey only one at a time, is also much less than that of seastars, which can eat many prey per meal (Paine 1971). Moreover, whelk propagules (benthic lecithotrophic larvae) have low dispersal abilities while seastar propagules (planktotrophic larvae) have high dispersal abilities. Thus, while on local scales (several square metres, Fig. 15) at a productive site, whelk density increased dramatically after large increases in prey abundance, at larger spatial scales (100's of square metres) and/or less productive sites, their abilities to control mussels seem weak. In contrast, both small- and large-scale seastar removals at such locations are likely to result in relatively uniform, large, and more persistent increases in prey. In other words, keystone predation may also vary with the spatial scale over which the predator operates. While whelks may sometimes compensate for reduced seastar predation, their impact on prey is likely to be substantially less than that of seastars. In the *-Pisaster* plots at SH exposed, therefore, whelks probably play a role more like that of gulls on Tatoosh Island, Washington (Wootton 1993): they may affect rates of succession by influencing the abundance of *M. trossulus* and barnacles, but seem unable to prevent a monoculture of California mussels.

Variation in interaction strength

The strength of the interaction between *Pisaster* and *Mytilus* varied on at least three spatial scales (<10 m = "microscale"; 100's of metres = "mesoscale"; and 10's of kilometres = "macroscale"). At some sites, mussel mortality in clumps located only metres apart differed greatly, indicating high short-term, microscale variation in interaction strength. Predation rates were consistently low at wave-protected sites compared to wave-exposed sites, suggesting consistent patterns of mesoscale variation in interaction strength. Predation intensity was also far lower at BB than at SH, suggesting striking macroscale differences in interaction strength.

In contrast to the high degree of spatial variation in predation, temporal variation appeared low. Results of transplant experiment were similar in 1990 and 1991 (Figs. 7 and 9), and unquantified observations since the mid 1980s suggest that the time course of predation varies little among years.

What were the causes, or mechanisms of these differences in interaction strength? Understanding the causes of variation in interaction strength depends on evaluating the causes of variation at three spatial scales.

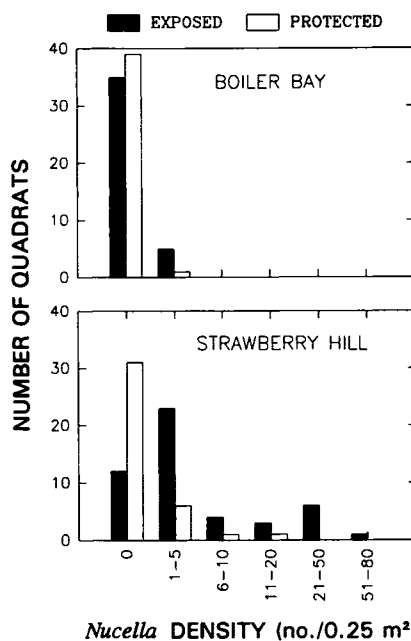


FIG. 17. Dispersion of whelks at each site \times exposure combination in June 1990 prior to manipulation. Bars show number of 0.25-m² quadrats (n 's; BBE, 40; BBP, 40; SHE, 48; SHP, 39) with the number of *Nucella* spp. listed on the abscissa. Comparisons to a Poisson probability (random) distribution (Sokal and Rohlf 1981) indicates SH whelks were nonrandomly distributed. Since both sites had quadrats with high whelk numbers, *Nucella* spp. distribution was clumped. At BB, whelks were randomly distributed at the exposed location, and too rare to test at the protected location.

At the smallest spatial scale, for instance, predation varied with local seastar abundance. When seastars were scarce, some clumps would be eliminated while others remained undetected, causing a high variation in mussel survival (Fig. 8). When seastars were abundant, all clumps were detected and eliminated almost simultaneously (e.g., Fig. 8).

Mesoscale and macroscale variation in predation were also correlated with seastar density. Predation rates were greatest where *Pisaster* was most abundant and lowest where *Pisaster* was least abundant (correlation coefficient between seastar density and predation rate in mussels eaten per day = 0.989; Table 1 in Menge 1992). Seastars were denser and therefore predation rates were higher at wave-exposed than at wave-protected sites (a scale of 100's of metres), and at SH than at BB (a scale of 10's of kilometres).

What are the causes of variation in seastar density? Likely factors include variation in stress and short-term habitat instability from sand burial, heat and/or desiccation stress, and food supply.

Stress from sand burial.—Periodic incursions of massive volumes of sand evidently influenced variation in interaction strength, at least at SH protected. Here, sand incursions usually occur in July and persist through October or November. Considerable short-

term variation can occur within this annual pattern, however. Substantial increases and decreases in sand cover were observed to occur in a matter of days at SH protected. Moreover, sand burial can occur "out-of-season." In 1992 and 1993, for instance, incursions of, and shifts in the depth of sand cover were observed in late winter and spring. Thus, at SH protected, sessile organisms were annually threatened with smothering, the probability of which varied unpredictably in space and time. These observations coupled with the mussel transplant experiment results (Figs. 7, 9, and 10) suggest that organisms at SH protected live in a suboptimal habitat in which highly stressful physical conditions greatly weaken interaction strength, particularly between seastars and their prey.

Field observations were consistent with this conclusion. Mobile organisms such as seastars avoided burial by either crawling higher on rocky outcrops or crawling on the surface of the sand. Crawling on sand, however, carries a high risk of damage or mortality. Since seastar sensory capabilities do not allow detection or prediction of the direction or distance to the nearest rock surface (required for firm attachment) across a sand surface, the probability of being caught in and rolled around by waves during flood tide is unpredictable. Observations both of seastars crawling on sand and of unhealthy or moribund individuals of *Pisaster* lying on sand was a regular (but not a frequent) event at SH protected, but was rare elsewhere. Thus, while mortality from sand burial may be infrequent at SH protected, shifting sand may both disrupt foraging activity and feeding of seastars (and other mobile invertebrate predators), and impose direct and indirect physical and physiological stresses.

Food input.—A second factor, low food supply, may be another cause of variation in interaction strength. First, mussel recruitment (Fig. 13) and prey growth (Fig. 14, Menge 1992) were both low at protected areas, implying that food input was low. Moreover, predation intensity (mussels eaten per day) was highly correlated with mussel recruitment (cumulative recruits per 100 cm²), mussel growth, and barnacle growth (Table 1 in Menge 1992). This is consistent with the suggestion that low interaction strength at protected sites resulted in part from low food supply.

1. **Low predation at SH protected.**—In addition to helping explain variation in predation intensity between locations differing in wave exposure, the relative contribution of low food supply at protected areas probably varied between sites as well. For example, at SH protected, low food supply may have been influenced directly by sand burial as well as by low prey recruitment and growth rates. Thus, most mid intertidal rock substratum below the high sand level was usually almost completely bare, probably because sand burial kills those few prey managing to recruit to this particular habitat. Evidence for this interpretation comes from observations of mass mortality of bands

of barnacles at the lower edge of the barnacle zone at the most protected areas at SH (no mussel bed occurs this far in from the shore edge). Field observations indicate such mortality occurred because sand levels temporarily reached somewhat higher than normal levels and killed barnacles that had settled and grown during sand-free periods.

The other important seastar prey, adult mussels, were virtually never observed in low intertidal barren areas, except for clumps that had probably exfoliated from more seaward mussel beds and were washed landward, and our experimentally transplanted clumps. Naturally exfoliated clumps sometimes reattached and survived for a few weeks or months, but were eventually either eaten by seastars or, more often, smothered by sand. As discussed earlier, data from experimental clumps directly indicate that mussels were intolerant of sand burial (Fig. 10). Thus the barrenness of the rock surfaces at SH protected apparently results from sand burial killing most sessile animals, thereby creating a very food-poor habitat for invertebrate predators. We conclude that weak interaction strength at SH protected results from low recruitment, low prey growth, and several effects of physical stress (inhibiting foraging activity, making prey inaccessible, reducing prey abundance). These factors are probably the most important in controlling community structure.

2. **Low predation at BB protected.**—Low food input may also have caused variation in interaction strength at BB protected, but this factor may not be sufficient to explain the results. While *Pisaster* can potentially eliminate *M. californianus* from the low zone, under normal conditions the primary factors preventing the low zone from even approaching mussel dominance may be low prey recruitment and slow prey growth, possibly combined with diffuse predation (by whelks, seastars, and conceivably other predators). For instance, the few seastars that moved through +*Pisaster* plots were evidently sufficient to eventually eliminate most transplanted mussels. Longer term observations of the experiments shown in Figs. 7 and 9 revealed that most mussels had been eaten by the following winter, although a few bivalves from 1991 clumps persisted at least 21 mo (some 1990 mussels survived 12 mo but were then collected to measure growth; Fig. 14). Thus, in the low zone at BB protected, it seems unlikely that adult *M. californianus* could survive indefinitely without protection from predators.

However, while low, some mussel recruitment did occur at BB protected (Fig. 13), and barnacle recruitment was often moderately high (B. A. Menge, *unpublished data*). Nonetheless, no increases in abundance of these prey occurred in the absence of seastars (B. A. Menge, *unpublished data*). Further, no increase in California mussels has yet occurred due to downward movement from mid intertidal zone beds like that seen at exposed sites and in Washington (Paine 1974). Why didn't prey abundances increase in -*Pisaster* treat-

ments? A possible explanation is that diffuse predation kept these prey in check at BB protected, although experimental artifacts are an alternative possibility. We consider these in turn.

a. *Other predators.*—Although we suggested above that *Nucella* spp. are unlikely to be keystone predators, results at SH exposed and the following observations indicate whelks might be important predators at BB protected, particularly when seastars are scarce. First, although whelks were not abundant at BB protected (Figs. 15 and 17), those present were regularly observed feeding on barnacles, usually within 1–2 m of the lower edge of the mussel beds. Second, whelks are present year-round while seastars are often nearly absent from this site for months at a time. Third, whelks have been shown to check prey populations elsewhere (Connell 1970, Dayton 1971; E. Berlow and S. Navarrete, *unpublished data*), so it is possible that these animals have a similar effect at this sheltered site in Oregon. Fourth, at BB protected, factorial-design experiments (with and without seastars and whelks, respectively) indicated transplanted *M. trossulus* suffered significant mortality from whelks (S. Navarrete and B. A. Menge, *unpublished data*). Further, while large *M. californianus* seem safe from whelk predation, small California mussels are probably susceptible to whelk attack.

While crabs or fishes are unlikely to be important predators at wave-exposed sites or SH protected, the possibility that these predators affect prey at BB protected cannot be ruled out. Anglers sometimes catch surfperch at this site, for instance. Although no evidence of crab predation was observed at this location, crabs may reside subtidally and forage intertidally at high tide as has been seen elsewhere (e.g., Kitching et al. 1959, Lubchenco and Menge 1978, Menge 1983; S. Yamada, *unpublished data*). Thus at BB protected, low recruitment, slow prey growth, whelk and seastar (and/or possibly crab and fish) predation may all combine to limit mussel populations.

b. *Potential artifacts.*—Although these experiments may not have lasted long enough to detect changes at BB protected, the evidence weighs against this alternative. For instance, the potential recruitment season of barnacles, an early successional species (e.g., Dayton 1971, Paine and Levin 1981, Farrell 1991) was lengthy, from February through December (B. A. Menge, *unpublished data*). Both *Balanus glandula* and *Chthamalus dalli* settled frequently and often heavily on recruitment plates at this site. This, and the fact that we maintained these experiments for four successive seasons (1990–1993) suggests we should have seen at least short-term increases of barnacles in the absence of seastars.

Additionally, although insufficient time may explain why mid zone *M. californianus* did not move downward in the absence of seastars at BB protected, another alternative seems more likely. Here, mid zone mussel beds were patchy, discontinuous monolayers ($\approx 30\%$

cover), had rather high levels ($\approx 40\%$) of unoccupied space, and consisted of relatively small individuals (3–6 cm). Perhaps, due to slow growth and low recruitment, these beds do not experience strong lateral between-mussel pressures like those at more crowded wave-exposed sites ($\approx 90\%$ cover). In other words, the forces causing downward cascading of mussel beds (crowding, recruitment, and growth) at exposed areas may be weak at BB protected.

Another possible artifact is that seastar removal was ineffective at BB protected; rapid re-invasion may have equalized seastar predation in $-Pisaster$ plots and $+Pisaster$ plots. While (as noted above) we did not completely exclude seastars, this possibility also seems unlikely. First, “background” mortality rates in $-Pisaster$ plots were lowest at BB protected. Fewer seastars reinvaded BB protected than any other site (Appendix), and survival of mussels in the absence of *Pisaster* at BB protected was either higher (1990) or equal (1991) to that at BB exposed. Second, seastars feeding on mussel clumps were observed about three times more often in $+Pisaster$ plots than in $-Pisaster$ plots (Table 6). Moreover, feeding seastars continued feeding in $+Pisaster$ plots but were removed in $-Pisaster$ plots. Third, since this was the most accessible site during heavy wave conditions, monitoring was actually somewhat more frequent at BB protected than at other sites. Finally, at the end of the experiment, mussel survival in the presence of seastars was significantly less than in their absence (Figs. 7 and 9), clear evidence that predation was stronger in $+Pisaster$ plots than in $-Pisaster$ plots. We conclude these potential artifacts did not compromise our results and therefore suggest predation at this site was diffuse and moderately strong.

In summary, at wave-exposed sites, *Pisaster* was evidently a keystone predator. Similar results in Washington and qualitative observations at other headlands suggests this seastar fills this role at many if not most such habitats where it co-occurs with California mussels. At wave-protected sites in Oregon, however, and probably at many other similar habitats along the Pacific coast of North America (e.g., Paine 1980, Robles 1987, Foster 1990, Robles and Robb 1993), the strength of its effect on prey diminishes. Where prey input is low, predation may still be strong but diffuse, and this seastar may be just one member of a predator guild that together prevents increases in prey abundance. With both low prey input and severe environmental stress (sand burial), predation appears weak and unimportant in preventing prey increases.

GENERAL DISCUSSION

Variation in predation in other habitats: implications for the keystone species hypothesis

Our suggestion that *Pisaster ochraceus* is a keystone predator in some subhabitats but not in others raises

two questions. First, is similar variation seen in other habitats, both marine and non-marine? Second, are there clearly discernible properties of the species, systems, or habitats that distinguish keystone from non-keystone species? Examples from other habitats, mostly aquatic, suggest that both keystone and nonkeystone or "diffuse" predation are widespread, and that prey production rates may be the primary factor underlying variation in keystone predation.

Rocky shores.—Two examples evinced within-system variation similar to that seen in Oregon. At intermediate to sheltered sites in New England, mid intertidal community structure appeared controlled by the whelk *Nucella lapillus*, despite the presence of other predators (Menge 1976, 1978a, b, 1982a, 1991b; see Edwards et al. 1982, Petraitis 1990 for alternative viewpoints). In contrast, low intertidal community structure was evidently determined by a guild of predators (whelks, seastars, and crabs), no one of which was consistently dominant (Lubchenco and Menge 1978, Menge 1983). Hence, mid and low zones were characterized by keystone and diffuse predation, respectively.

Similar variation was observed in southern California (Robles 1987, Robles and Robb 1993). High sheltered and mid-exposed community structure depended on keystone predation (by lobsters), and mid-sheltered community structure depended on diffuse predation (mostly by lobsters and whelks).

Other rocky intertidal examples are available but with one possible exception, within-system variation was not evaluated. Keystone predation was observed in New Zealand (Paine 1971), where a seastar controlled mussel zonation with little apparent impact of other predators, and in Chile (Durán and Castilla 1989), where a large predatory gastropod evidently controlled mussel abundance and zonation in the mid intertidal zone. The potential exception is that in Chile, seastar removal experiments in the low zone yielded only modest increases in mussel abundance (Paine et al. 1985). Since other predators were present, mussel increases may have been small because this was a diffuse predation system, but we cannot presently assess this possibility.

Diffuse predation was suggested in two other studies. In Panama, with low prey recruitment, total predator exclusion (fishes, molluscan grazers, crabs, and whelks) produced large increases in prey, while single predator exclusions produced little to no change (Menge and Lubchenco 1981, Lubchenco et al. 1984, Menge et al. 1986a, b, Menge 1991a). In Ireland, crabs, seastars, and whelks apparently combined to limit mussels to wave-exposed shores (Kitching et al. 1959). Although other predation studies have been done (e.g., Connell 1961, Fairweather 1985, Dungan 1986, 1987), whether predation was keystone or diffuse cannot be evaluated.

Subtidal habitats.—In some subtidal habitats (Alaska, possibly central California), keystone predation by

sea otters evidently controlled sea urchins and thereby indirectly maintained dense kelp beds (e.g., Estes and Palmisano 1974, Estes et al. 1978, Estes and Harbold 1988, Van Blaricom and Estes 1988, Estes and Duggins 1995). Elsewhere, dense kelp beds existed in the complete absence of sea otters, suggesting sea urchins were controlled by other factors, possibly including different predators (Foster and Schiel 1988). In the tropics, the seastar *Acanthaster planci* can alter community structure dramatically during population outbreaks (e.g., Colgan 1987), and in such cases appears to be a keystone predator. However, this effect is sporadic in time and space and may be relatively minor compared to other factors (e.g., Glynn 1976, 1988, Connell 1978, Wellington 1982, Hixon and Brostoff 1983, Glynn and D'Croz 1990). Finally, in South Africa, rock lobsters control mussels on one island (Malgas Island), but are eliminated on nearby Marcus Island by whelks, evidently resulting in high mussel abundance (Barkai and Branch 1988, Barkai and McQuaid 1988). Both lobsters and whelks thus appear to be keystone predators. Curiously, the same whelk species is a lobster prey on Malgas Island. The initial cause of the persistent differences between these communities remains unknown.

Soft-sediment marine habitats.—Experiments in soft-sediment communities have demonstrated the entire range of predation regimes. Predation has ranged from weak to strong, and from single keystone predators to guilds of predators (e.g., Peterson 1979, Hall et al. 1990, Wilson 1990, Kvitek et al. 1992). A major departure from the keystone paradigm, however, is the apparent absence of dominant competitors capable of excluding prey. Thus, in the absence of predation, most soft-sediment studies documented large increases in prey abundance or biomass (and often increased diversity) but no emergence of a single dominant prey (or decreased diversity). This may result from the absence of solid surfaces that could be monopolized by competitively dominant species (Peterson 1979).

Non-marine habitats.—In high Rocky Mountain ponds, larval salamanders were apparently keystone predators having major effects on zooplankton size and species composition (Dodson 1970). In experimental pond communities in New York, bluegill sunfish (*Lepomis macrochirus*) evidently played a keystone role (Hall et al. 1970). In temporary ponds in the southeastern USA, newts have major effects on abundance and species composition of tadpole populations (Fauth and Resetarits 1991). Another salamander had no influence on the effects of the newt on prey species composition (but strongly affected abundances), leading these workers to conclude that newts were keystone predators. In lakes, largemouth bass (*Micropterus salmoides*) manipulations produced dramatic community changes (a "trophic cascade"; Carpenter et al. 1987). Other large fishes were evidently present (although scarce) so bass were probably a keystone predator. Other lake communities are also evidently structured by

single species of large piscivorous fish (e.g., Mills and Forney 1988, Persson et al. 1988), but it is not clear in these examples if other piscivores were present. Some lakes have several piscivores as top predators (e.g., McQueen et al. 1989) but the predation regime has not been evaluated. In streams, two fish species were top predators (Power 1990, 1992). Manipulations tested total predation, not single predator effects, however, so whether predation was keystone or diffuse cannot be ascertained.

Few examples are available from terrestrial habitats. On small islands, a lizard guild (*Anolis* spp., *Ameiva festiva*) controlled insect and spider populations, thereby alleviating grazer impacts on the vegetation (Spiller and Schoener 1988, 1990a, b). While diffuse predation is suggested by these results, keystone predation was not tested. Other relevant terrestrial studies similarly imply that diffuse predation controls community structure (e.g., Erlinge et al. 1984, Kotler 1984, Brown et al. 1986, Brown and Heske 1990), although the critical experiments have not yet been done to evaluate either possibility. Bond (1993) suggests that large mammalian carnivores in African game reserves may be keystone predators of their herbivore prey, but no tests of this idea or of the diffuse predation alternative are available. From a somewhat different perspective, Strong (1992) argues that terrestrial systems are primarily diffuse predation systems because they are usually high-diversity systems. Nonetheless, the frequency of keystone predation in terrestrial habitats is presently unclear.

Hence, at least in aquatic environments, keystone predation is common but not universal since diffuse predation also seems common. Thus, any general synthesis of the conditions under which predation controls community structure should consider both causes of variation in interaction strength and in predation mode (keystone or diffuse).

Are keystone predators unique?

Are keystone predators distinct from other predators? What are the unique properties of keystone predators, if any? Using *Pisaster* as his model, Paine (1969, 1977) proposed that keystone predators selectively consume competitively superior prey that could potentially eliminate other organisms (Table 9). Other possible characteristics are that keystone predators are large relative to prey, have high functional and/or numerical responses, have indeterminate growth, and have high mobility and thus a relatively large foraging range (e.g., Paine 1976, Menge 1982b; Table 9). Keystone systems potentially have prey refuges in space or size, space as the primary limiting resource in competition, high food input rates, subdominant competitors with higher recovery rates than dominant competitors, and low diversity (Menge 1982b, Strong 1992; Table 9).

Since knowledge of all these properties is rare, available evidence is uneven. Table 10 lists some aquatic

TABLE 9. Postulated properties of keystone predators and keystone systems.

Property	Reference
Keystone predators	
1. Selective or differential predation on dominant prey	Paine 1969, 1977
2. Major prey is competitively dominant to all other prey	Paine 1969, 1977
3. Large body size relative to prey	Hall et al. 1970
4. High functional, numerical responses	Menge 1982b
5. Indeterminate growth	Hall et al. 1970 Paine 1976
6. Predator has high mobility, large foraging range	Menge, 1982b
Keystone systems	
7. Prey refuges in space	Paine 1966, 1974
8. Prey refuges in size	Paine 1976
9. Space is the primary limiting resource in competition	Paine 1977
10. High rates of food input	this paper
11. Subdominant competitors have higher recovery rates than dominant competitors	this paper
12. Low diversity	Strong 1992

studies for which many of the above properties were known. With two exceptions, comparisons suggest no consistent pattern for any characteristic (Table 10). The exceptions are that (1) dominant competitors existed in all examples of strong predation, but occurred in both keystone and diffuse predation systems, and thus do not uniquely characterize keystone systems, and (2) in marine systems, food input rates appear relatively high in keystone predation systems and relatively low in diffuse systems. We summarize our evaluation of properties 1–12 (Table 9) as follows.

Preferential/selective predation on a competitively dominant prey (property 1): Several have noted that disproportionate, and not necessarily preferential predation on a competitive dominant is sufficient to produce a keystone effect on prey (e.g., VanValen 1974, Yodzis 1977, Hixon 1986). With the exception of the New England mid intertidal zone, where whelks switched from barnacles to mussels, differential predation on the competitive dominant occurred in all known cases. However, disproportionate predation on competitive dominants occurred in both keystone and diffuse systems (Table 10), so keystone systems are not uniquely characterized by this property.

Property 2: Exclusion of other species by dominant competitor: This occurred in all cases listed (Table 10), but again, such competitors occur in both keystone and diffuse systems. In intertidal examples, bivalves were dominant competitors (Table 10). In subtidal habitats, dominant competitors include kelp, corals, and mussels (e.g., Estes et al. 1978, Colgan 1987, Barkai and McQuaid 1988). In freshwater examples, cladocerans appear to be dominant competitors in herbivorous zooplankton prey communities (e.g., Dodson 1970, Hall

TABLE 10. Summary of ecological characteristics of some keystone predation and diffuse predation communities in marine hard-bottom and freshwater habitats. "Yes" or "No" with a question mark indicates uncertainty in the conclusion. "Yes & No" means some of predator species have the characteristic and some do not. Question mark without 'yes' or 'no' means that characteristic is unknown.

System/ predator(s)	References*	Ecological characteristics†			
		1 Differential predation on competitively dominant prey	2 Major prey can exclude all others	3 Large pred./ prey size ratio	4 High func- tional/ numerical response ratio
KEYSTONE PREDATORS/SYSTEMS					
Marine habitats					
New England	1, 2, 3	Yes, but variable	Yes	No	No
Mid intertidal, intermediate to protected <i>Nucella lapillus</i> (whelk)					
Pacific Northwest	4, 5, 6	Yes	Yes	Yes	Yes
Mid/low intertidal, exposed <i>Pisaster ochraceus</i> (seastar)					
New Zealand	7	Yes	Yes	Yes	Yes
Mid/low intertidal, exposed <i>Stichaster australis</i> (seastar)					
Chile	8, 9	Yes?	Yes	Yes	No?
Mid/low intertidal, exposed <i>Concholepas concholepas</i> (whelk-like gastropod)					
So. California	10, 11	Yes	Yes	Yes	Yes
High intertidal, protected, mid intermediate <i>Panulirus interruptus</i> (spiny lobster)					
Alaska	12, 13, 14, 15	?	Yes	Yes	?
Subtidal <i>Enhydra lutris</i> (sea otter)					
South Africa	16, 17	Yes	Yes	Yes	Yes?
Subtidal <i>Jasus lalandii</i> (rock lobster)					
Freshwater habitats					
New York	18	Yes	Yes	Yes	Yes
Ponds <i>Lepomis macrochirus</i> (bluegill sunfish)					
Wisconsin	19	?	Yes?	Yes	Yes?
Lakes <i>Micropterus salmoides</i> (largemouth bass)					
New York	20, 21	?	?	Yes	Yes?
Lakes <i>Stizostedion vitreum vitreum</i> (walleye)					
Sweden	22, 23	?	?	Yes	Yes?
Lakes <i>Stizostedion lucioperca</i> (zander)					
DIFFUSE PREDATORS/SYSTEMS					
Marine habitats					
New England	24, 25	Yes	Yes	Yes & No	Yes
Low intertidal, intermediate to protected (whelks, seastars, crabs)					
Panama (Pacific)	26, 27, 28	Yes	Yes?	Yes & No	Yes
Intertidal (high, mid, low) (whelks, crabs, fishes)					

TABLE 10. Continued.

Ecological characteristics†							
5 Indeter- minate growth	6 High mobility	7 Space refuge	8 Size refuge	9 Space is limiting resource	10 High food input	11 Differential recovery	12 Low diversity
KEYSTONE PREDATORS/SYSTEMS							
Marine habitats							
No	No	Yes	No	Yes	Yes	Yes	Yes
Yes	Yes	Yes	Yes	Yes	Yes	Yes	No
Yes	Yes	Yes	?	Yes	Yes?	Yes?	No
No	Yes	Yes	No	Yes	Yes?	Yes	No
Yes	Yes	No	No	Yes	?	Yes?	No
No	Yes	Yes	No	Yes (kelp)	?	Yes?	Yes
Yes?	Yes?	Yes? (Marcus I.)	No?	Yes	Yes?	No	No
Freshwater habitats							
Yes	Yes	No	No	No (food)	?	?	?
Yes	Yes	No	No	No (food)	?	?	Yes?
Yes	Yes	No?	No?	No	?	?	?
Yes	Yes	?	?	No	?	?	?
DIFFUSE PREDATORS/SYSTEMS							
Marine habitats							
Yes & No	Yes & No	Yes	No	Yes	Yes, but < mid	Yes	Yes
Yes & No	Yes & No	No	No	Yes	No	Yes	No

TABLE 10. Continued.

System/ predator(s)	References*	Ecological characteristics†			
		1 Differential predation on competitively dominant prey	2 Major prey can exclude all others	3 Large pred./ prey size ratio	4 High func- tional/ numerical response ratio
So. California Mid intertidal, protected (whelks, lobsters, fish)	11	Yes	Yes	Yes & No	Yes & No
Ireland Mid/low intertidal, intermediate/protected (whelks, seastars, crabs)	29	?	Yes?	Yes & No	Yes & No
Freshwater habitats					
Canada Lakes (fishes: largemouth bass, pike, >10 cm perch)	30	?	?	Yes	Yes?
California River (fishes: roach, steelhead)	31, 32	?	?	Yes	Yes?

* 1 Menge 1976, 2 Menge 1978a, 3 Menge 1978b, 4 Paine 1966, 5 Paine 1974, 6 Paine 1976, 7 Paine 1971, 8 Paine et al. 1985, 9 Durán and Castilla 1989, 10 Robles 1987, 11 Robles and Robb 1993, 12 Estes and Palmisano 1974, 13 Estes et al. 1978, 14 Estes and Harrold 1988, 15 Estes and Duggins 1995, 16 Barkai and McQuaid 1988, 17 Barkai and Branch 1988, 18 Hall et al. 1970, 19 Carpenter et al. 1987, 20 Mills et al. 1987, 21 Mills and Forney 1988, 22 Persson et al. 1988, 23 Persson et al. 1993, 24 Lubchenco and Menge 1978, 25 Menge 1983, 26 Menge and Lubchenco 1981, 27 Lubchenco et al. 1984, 28 Menge et al. 1986, 29 Kitching et al. 1959, 30 McQueen et al. 1989, 31 Power 1990, 32 Power 1992.

† Numbers of ecological characteristics are as listed in Table 9.

et al. 1970, Carpenter et al. 1987). This property does not extend to soft-bottom communities, however, as noted above.

As indicated in Table 10, properties 3–9 and 11 either all have exceptions within the keystone predation systems, or occur in both keystone and diffuse systems (and thus do not distinguish predation regimes), or both. Property 12, that keystone systems have low diversity and diffuse systems have high diversity, is evidently not supported by the evidence either. This point deserves further comment.

First, rocky intertidal regions, among the most intensively manipulated communities, provide several exceptions to predictions of property 12. Pacific Northwest intertidal communities are renowned for their high diversity (e.g., Ricketts et al. 1985). As we have argued in this paper, the most diverse subhabitats in this region, wave-exposed sites, are where keystone predation occurs. When more sheltered, less diverse subhabitats are considered, predation is evidently either weak or diffuse. On a larger scale, keystone predation occurs in both low- (New England mid intertidal zone) and high-diversity communities (New Zealand, Chilean mid intertidal zone). Similarly, diffuse predation is also apparent in both low- (New England low intertidal zone) and high-diversity communities (Panama, possibly Chilean low intertidal zone; Table 10). Second, in terrestrial habitats, the few examples available (see *Non-marine habitats*, above) also seem counter to the hypothesis, since diffuse predation systems may exist in

both low-diversity (e.g., the lizard-dominated Bahamian island systems; Spiller and Schoener 1988, 1990a, b) and high-diversity communities (e.g., the desert-grassland system; Brown et al. 1986). Although evidence is limited, these observations are not consistent with the postulates of property 12, suggesting community diversity does not uniquely distinguish keystone from other systems.

These considerations leave high food input rates (property 10) as the final factor in our list that could distinguish keystone from nonkeystone systems. Evidence is also limited in this case, but seems consistent with the hypothesis. First, our studies in Oregon suggest that high prey production underlies the transition from a keystone to a diffuse predation community. Second, in Panama, a diffuse predation system, prey recruitment and abundance was very low in comparison to temperate areas (Menge 1991a). Third, the low intertidal zone in New England, a diffuse predation community, had relatively low prey recruitment and abundance, while the mid intertidal zone in New England, a keystone predation community, had relatively high prey recruitment and abundance (Menge 1991a). Thus, we hypothesize that keystone predation communities are distinguishable from diffuse predation communities by their relative rates of food input, which is a complex function of recruitment rates, growth rates, and perhaps ultimately, primary productivity (Menge 1992, Menge et al. 1994).

No other properties appeared to distinguish keystone

TABLE 10. Continued.

Ecological characteristics†							
5 Indeter- minate growth	6 High mobility	7 Space refuge	8 Size refuge	9 Space is limiting resource	10 High food input	11 Differential recovery	12 Low diversity
Yes & No	Yes & No	No	No	Yes	?	Yes	No
Yes & No	Yes & No	Yes	No?	Yes	?	?	?
Freshwater habitats							
Yes	Yes	?	?	No	?	?	?
Yes	Yes	Yes	No	Yes?	?	Yes?	Yes

from diffuse predation communities. However, in marine hard-bottom and freshwater habitats, when a system had strong predation, whether keystone or diffuse, it also appeared to have a dominant competitor, which in most cases experienced differential predation. Thus, these properties, proposed by Paine (1969) to characterize keystone systems, may in fact characterize a broader category of community dynamics; i.e., strong predation systems. These traits evidently do not typify marine soft-sediment communities, however, due to an apparent absence of competitive exclusion among infaunal prey (Peterson 1979, Wilson 1990). It is intriguing that competitive exclusion and/or dominance can be important in two types of space-limited system (marine hard bottoms, freshwater streams; two-dimensional spatial habitats) but not in another (marine soft bottoms; a three-dimensional spatial habitat). Equally interesting is that competitive dominance, if not exclusion, is important in freshwater planktonic communities, which are presumably food limited. Determination of the basis of these similarities and differences will be challenging.

The keystone species concept has contributed to several advances, including the concepts of interaction strength (MacArthur 1972), interaction or functional webs (Paine 1980, Menge and Sutherland 1987), food web theory (May 1973, Pimm 1982, Lawton 1992), and maintenance of biodiversity. Thus, while the term keystone species has often been used inappropriately, we do not agree that the concept "is largely undemonstrated in nature . . ." (Mills et al. 1993). Although they are not universal, the structure of many communities appears influenced, if not dominated, by keystone species. We thus argue the concept should be retained, but

placed in a broader context: communities may be affected by strong or weak predation, and those with strong predation may be under the influence of either keystone or diffuse predation. Moreover, food input rates, perhaps ultimately a function of primary production, may help distinguish which strong predation regime characterizes a community. Thus, as predicted by models of community regulation (e.g., Oksanen et al. 1981, Fretwell 1987, Menge and Sutherland 1987, Power 1992), interaction strength probably varies with underlying environmental gradients. Our study, with others (e.g., Sih et al. 1985, Menge and Farrell 1989, Wootton and Power 1993) indicates such models have some predictive capacity. Testing, modifying, and extending these models offer much promise for continued progress in community ecology.

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APPENDIX

Number of *Pisaster ochraceus* removed from removal plots at Boiler Bay and Strawberry Hill. ... = no data available. At Boiler Bay, columns are listed in order of wave exposure from left (most exposed) to right (least exposed). Strawberry Hill replicates are of similar wave exposure within sites.

Year	Dates	Boiler Bay				Strawberry Hill			
		Exposed		Protected		Exposed		Protected	
		Rep1	Rep2	Rep1	Rep2	Rep1	Rep2	Rep1	Rep2
1990	9, 11 June	60	21	20	12	426	369	106	17
	24, 25 June	5	3	8	1	85	80	2	3
	6, 7, 10 July	17	10	16	3	177	82	6	15
	21, 23 July	10	3	4	0	15	24	1	3
	6, 7 August	12	4	2	2	9	7	6	1
	19, 20 August	24	5	3	3	29	18	12	1
	5, 6 September	25	9	7	0	99	...	104	8
	5, 6 October	4	11	5	1	39	26	23	0
	3, 4 November	8	8	3	1	58	26	4	6
	1 December	64	41	10	10
1991	28, 29 January	0	3	2	7	70	57	4	2
	25, 26 February	0	0	0	0	39	30	3	0
	15 April	281	111	0	3
	1 May	55	31
	13, 16, 17 May	6	5	0	0	63	25	17	...
	13, 14 June	4	4	0	2	63	61	0	2
	25, 26 June	5	6	8	3	136	57	69	32
	27, 28 June	1	2	0	0	4	5	1	3
	11, 12 July	10	3	0	0	42	33	10	0
	26, 27 July	5	6	5	1	94	33	12	8
	10, 12 August	5	4	8	3	22	37	6	11
	23, 24 August	1	2	0	0	30	95	42	3
	8, 9 September	4	4	4	1	13	59	17	16
	9, 12 October	4	5	3	0	10	30
	22, 23 November	2	4	0	0	65	69	6	1
	18 December	6	24
1992	17 February	88	110	7	14
	15, 16 March	0	5	45	79	9	8
	Totals	212	122	98	32	2127	1619	477	167
	Sample dates (N)	21	21	22	22	27	26	24	23
Percent of the original number of individuals reinvading per sample date [means and (1 SE)]		12.1 (2.6)	22.9 (2.9)	17.7 (4.3)	12.5 (3.3)	14.8 (2.7)	13.0 (1.6)	14.6 (4.7)	38.4 (9.2)