Chapter 2

The Overriding Importance
of Environmental Context
in Determining the Outcome
of Species-Deletion Experiments

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Classic ecological experiments such as those of Paine (1966, 1974) leave little doubt that species loss can have profound consequences on a community. At the same time, there can be striking variation in these consequences. Thus, to understand the consequences of a loss of species from a community, one must learn the factors that are responsible for the variation observed in studies of removals, losses, introductions, or invasions of species. An ultimate goal in such efforts is prediction: can we forecast what will happen when a species is deleted from a community or ecosystem? It is still far from clear whether a meaningful prediction can be made of population or community consequences of species loss. The most that we can accomplish may be to understand the changes that have occurred and, from

this understanding, make only general predictions of the outcomes of activities that are likely to lead to species loss.

Predicting the outcomes of species loss depends on discovering the rules that regulate species interactions and their aftereffects, and how these vary with environmental conditions (Belyea and Lancaster 1999). My goal in this contribution is to probe a small part of this issue. My primary focus is on environmental context, both abiotic and biotic, and the extent to which it dictates the aftermath of species loss in natural communities. Because a vast literature has developed on the consequences of species loss, here I restrict myself largely to examples that involve consumers in marine hard-bottom communities. Much of my treatment summarizes and synthesizes examples taken from my own research activities during a 30+-year career that was launched with the guidance and insights of my dissertation advisor and mentor, Bob Paine. It is with the deepest respect that I dedicate this paper to Bob on the occasion of his retirement from the Department of Zoology at the University of Washington. The debt I owe him is large. My career-long focus on the factors that structure and regulate ecological communities was given its initial push—plus numerous prods along the way—by Bob.

Concepts of Species Impact

Species are far from equivalent in their impacts on communities. This fact was revealed clearly by Paine's sea star manipulations in Washington, New Zealand, and Chile (Paine 1966, 1971, 1974; Paine et al. 1985). The keystone species concept that was fostered by this work (Paine 1969a) has become an integral feature of ecological theory and practical application, particularly in some schemes of ecosystem management (Mills et al. 1993). Despite recent controversy (Mills et al. 1993; Paine 1995; Power et al. 1996b), the concept is robust and broadly relevant (Menge and Freidenburg 2001). As was clarified recently, a keystone species is one "whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance" (Power et al. 1996b). An important implication of this definition is that keystone species have relatively high per capita interaction strengths—a quality that, when translated to the community level, is termed "community importance." Other concepts of species impacts include "dominant species," "strong interactors," and "weak interactors." Dominant species are those that have large effects on community or ecosystem structure but whose impact is a function of their high abundance or biomass. Such species would therefore have rela-

tively low per capita or per biomass interaction strengths, depending on the metric. By the definition followed here, strong interactors include keystone species, dominants, and all other species that have a large impact on populations as well as communities or ecosystems. Weak interactors are those that have little influence on any level of organization. This does not mean, however, that weak interactors are always unimportant in community dynamics. Under certain conditions, some weak interactors may increase their impacts on species dramatically, temporarily becoming strong interactors (Berlow 1999; Navarrete and Menge 1996). In other cases, many individual weak interactors together can jointly have strong impacts. An example is "diffuse predation," in which a guild or group of predators can collectively exert "strong" predation even though each by itself has a small effect (Hixon 1991; Menge et al. 1986a, 1994; Robles and Robb 1993).

Spurred in part by recent critiques of the keystone species concept, and by Paine's experimental analysis of interaction "strength" in a guild of molluscan herbivores (Paine 1992), ecologists have begun to quantify the magnitudes of species effects on per capita and per population bases (Berlow et al. 1999; Fagan and Hurd 1994; Navarrete and Menge 1996; Raffaelli and Hall 1996; Ruesink 1998; Wootton 1997; Harley, this volume). Although still in its infancy, this work has begun to quantify community patterns inferred long ago by Paine (e.g., Paine 1980): communities consist of a few strong interactors and many weak interactors. What remains unclear, however, are the ecological and evolutionary bases for differences in ecological impact among species. For example, what are the ecological mechanisms and evolutionary conditions that produce keystone species?

Environmental Context: A Primary Determinant of Species Impact

Much evidence suggests that variation among species in their impact, and thus in the consequences of their loss to the community, is determined by environmental context (e.g., Harley, this volume). By environmental context, I mean both abiotic and biotic environments. Abiotic context, for example, can include regimes of stress, disturbance, or productivity. Biotic context includes characteristics of the assemblage in which a species carries out its activities, such as diversity, species composition, traits of specific interactors, or the rate of replenishment (e.g., recruitment, growth) of resources. To simplify the discussion, I discuss each of these categories of environmental context

separately, although they are of course usually tightly interlinked in determining the outcome of species impacts.

Physical Context

As John Sutherland and I have argued, a variable regime of environmental stress can lead to dramatic differences in the outcome of species deletions (Menge and Sutherland 1987; see also Dunson and Travis 1991; Grime 1977). As on most rocky shores, for example, sites in New England occur along striking gradients in wave forces (horizontally along the shore) and exposure to air (vertically on the shore). The varying physical regime along these gradients leads to large differences in the impact of the predatory whelk *Nucella lapillus* (Menge 1976, 1978a, b; Menge and Sutherland 1976).

ENVIRONMENTAL CONDITIONS: HYDRODYNAMIC FORCES AND THERMAL STRESS

New England Shores. New England rocky intertidal regions harbor communities that have relatively few species, each of relatively high abundance (Dudgeon et al. 1999; Lubchenco and Menge 1978; Menge 1976). Zonation is sharply defined and varies with wave exposure. In wave-exposed areas, there are high-barnacle (*Semibalanus balanoides*), mid-mussel (*Mytilus edulis*), and low-mussel-kelp zones (*M. edulis* overlaid by a canopy of *Alaria esculenta* during the summer). On shores with intermediate exposure to waves, zones from high to low are dominated by barnacles, fucoids (*Fucus evanescens* [formerly *F. distichus*] and *F. vesiculosus*) overlying a mosaic of mussels and free space, and red algal turfs (*Chondrus crispus*, *Mastocarpus stellatus*). At more sheltered sites, zones are dominated by barnacles, the fucoid *Ascophyllum nodosum* overlying largely free space, and *Chondrus crispus* turfs. In the middle and high zones at intermediate to wave-exposed sites, the only predator is the whelk *Nucella lapillus*. In more sheltered areas, *Nucella* is joined by small individuals of the green crab (*Carcinus maenas*), and in low zones in intermediate and sheltered areas by sea stars (*Asterias forbesi*, *A. vulgaris*) and brachyuran crabs (*Carcinus maenas*, *Cancer irroratus*, *C. borealis*).

Using cage exclosure experiments in the high and middle zones of high and intermediate wave exposure, I found that predation by whelks varied strikingly (Menge 1976, 1991; fig. 2.1). In high zones, whelks had no effect on barnacles. Similarly, in mid-exposed zones, whelks had no effect on barnacles or on mussels. In sharp contrast, whelks had strong
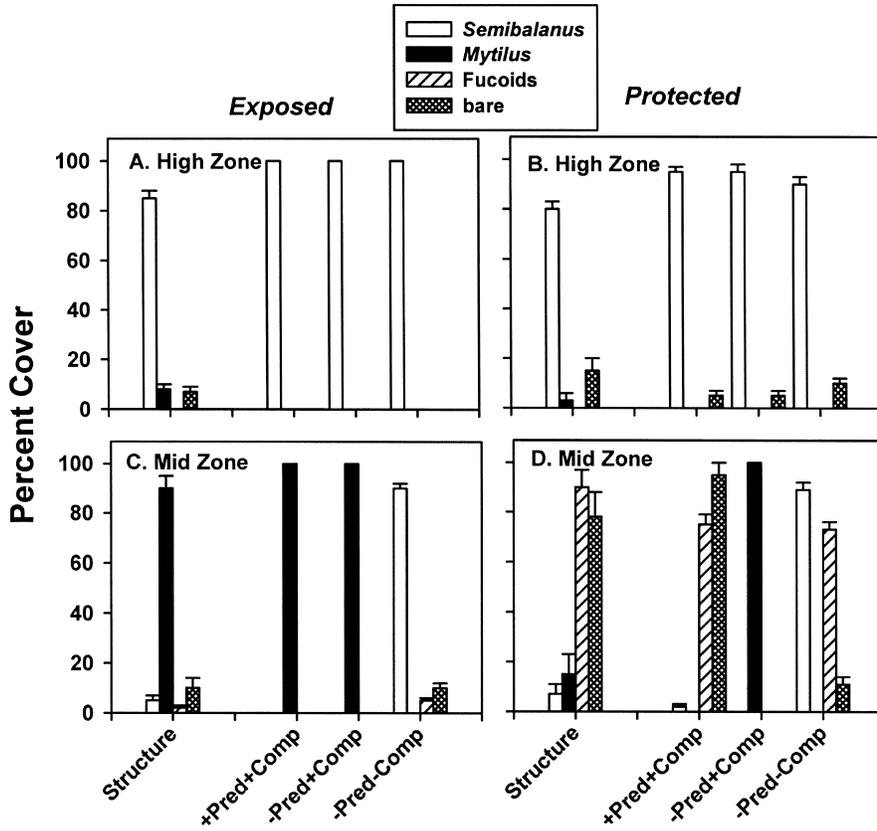
Figure 2.1 Summary of studies of community dynamics along a wave-exposure gradient in New England (after Menge 1976). Patterns of community structure are shown with the left set of histograms in each panel. Results are summarized from experiments in high (A, B) and mid (C, D) zones of different combinations of predation and competition among dominant space occupiers (presented as average abundance at the end of the season; generally autumn). In the high zone, neither predation nor interspecific competition affected community structure, regardless of exposure. In the mid zone, interspecific competition was the major determinant of community structure at exposed sites, whereas predation was the major determinant of community structure at protected sites. Error bars in this and the other figures are standard errors of the mean.

effects on both prey species in the intermediate mid-zones and, with algal whiplash, were the major determinants of low mussel and barnacle cover in such areas.

Field observations led me to surmise that physical constraints were the basis of subhabitat differences in the effects of whelks. To test this hypothesis, experiments quantified predation in relation to wave exposure, height on the shore, and other factors such as canopy cover (Menge 1978a, b). These experiments showed that whelk foraging rates were reduced greatly under conditions of high wave action and at higher shore levels. Foraging was decreased further when the canopy was removed, and whelks suffered high mortality under high-shore, canopy-free conditions. Although physical conditions could be evaluated only crudely in those days, it seemed clear that whelk foraging activity was inhibited by turbulent conditions at wave-exposed sites and by exposure to heat and desiccation stress higher on the shore. Later studies have confirmed the susceptibility of whelks to hydro-dynamic and thermal stress (e.g., Bertness et al. 1999; Dahlhoff et al. 2001; Denny 1988; Garrity 1984; Leonard et al. 1998). Thus, the role of *Nucella lapillus* in controlling the abundance and zonation of barnacles and mussels and, indirectly, of algae in mid-zones, was contingent on environmental conditions. Predation was weak where thermal or desiccation stress and hydrodynamic forces were great, whereas it was strong where these factors were more moderate.

Oregon Coast. Studies of the keystone species *Pisaster ochraceus* in Oregon have offered further insights into how species impact varies with abiotic context (Menge et al. 1994, 1996). As demonstrated by the studies of Paine (1966, 1974) and Dayton (1971), *P. ochraceus* can have overwhelmingly powerful effects on prey populations and community structure. Observations along a wave-exposure gradient on the Oregon coast, however, suggest that the impact of this predator on its prey varied under some conditions. In particular, in some subhabitats (e.g., wave-sheltered areas), sea stars were so scarce that it seemed unlikely that they played a major role in determining the lower limit to the mussel bed and low-zone community structure. In other subhabitats, sea stars were abundant, but sand burial appeared to be an alternative—or the only strong structuring agent in the low intertidal zone. Both situations were located in relatively wave-sheltered conditions.

Because the outcome of standard exclusion experiments can be contingent on the rates of prey recruitment (see section on oceanographic context), prey-transplant experiments were established as an alternative and supplementary approach for studying sea star preda-

tion. Mussels (*M. californianus*, the preferred prey of *Pisaster*) were transplanted from mid-zone beds to low intertidal regions (where these bivalves are normally almost absent) to plots with and without *Pisaster* (+sea stars and −sea stars, respectively). Experiments were conducted at wave-exposed and wave-protected areas at each of two sites. Predation was quantified by determining the rate of loss of mussels in +sea star and −sea star plots. To quantify variation in per capita interaction strength, the rate of mussel loss was standardized to a per–sea star basis (Menge et al. 1996). At Boiler Bay, an area with little sand transport in sheltered areas, per capita predation rates were relatively low in wave-exposed plots and relatively high in wave-protected plots. These per capita rates were related inversely to the abundance and predation impact of sea stars, which were both greater at wave-exposed areas. This result suggests that the foraging activity of individual *Pisaster* was less at wave-exposed than at wave-protected sites, just as was found for whelks in New England and on Tatoosh Island in Washington State (Quinn 1979).

Similar experiments at the other site, Strawberry Hill, also showed that per capita predation rates were lower at wave-exposed sites, suggesting that feeding may be reduced by hydrodynamic forces. These experiments at Strawberry Hill also revealed that another abiotic process—sand transport and the resulting periodic burial of wave-protected low intertidal areas—could override the influence of *Pisaster* in determining low-intertidal community structure. In such areas, mussel mortality in transplant experiments occurred at similar rates in plots with and without sea stars. Quantification of mussel survival in relation to sand burial suggested that, although mussels could apparently tolerate periods of a few weeks of burial, sand smothering was the dominant cause of death of the transplanted mussels. More generally, field observations from more than a decade of research at this site indicate that sand burial is the primary agent that structures low-intertidal communities over large areas of relatively wave-sheltered rocky shore. The usual absence of mussels and the barnacle *Balanus glandula* are determined largely by burial events, whereas sand-tolerant algae (e.g., *Gymnogongrus linearis*, *Laminaria sinclairii*), surfgrass (*Phyllospadix scouleri, P. torreyi*), and barnacles (*Chthamalus dalli*) persist as community dominants. Persistent populations of *Pisaster* occur in the area and often aggregate around and feed on clumps of *M. californianus* that have been dislodged from wave-exposed reefs to seaward. Other observations suggest that these "times of plenty" can have a severe cost, however. Sea stars in these areas are often found clustered on the tops of buried rock outcrops, lying moribund or dead on the substratum (with evidence of damage from tumbling about

over sand and rocks) or attempting to crawl on the sand away from recently buried outcrops. Because *Pisaster* is adapted for living on hard surfaces (its tube feet have suckers that are useless on sand), wave-sheltered areas at Strawberry Hill appear to be a suboptimal habitat.

Thus, although much evidence suggests that *Pisaster*'s role as a keystone species is probably general in a biogeographic sense, its community impact is clearly variable (see also Harley, this volume) and is contingent on both hydrodynamic forces and substratum stability. Curiously, the strongest effect of this sea star occurs in those habitats in which individual foraging appears to be most inhibited by wave turbulence. The Oregon studies suggest that the large impact of *Pisaster* at wave-exposed areas is a function of the higher density of sea stars. Possible reasons for this higher density are considered later (see "Biotic Context").

Other Examples. Physical constraints are widely known to influence the impact of marine species; examples range from whelks on temperate and tropical rocky shores (Quinn 1979; Garrity 1984; Garrity and Levings 1981) to echinoderm predators (Lawrence 1990; Witman and Grange 1998). Similarly, the idea that the physical environment limits the likely impact of species removal is also thought to apply widely in terrestrial communities from biogeographic to local scales (Collinge and Louda 1988; Gillette 1962; Louda 1982; Louda and Collinge 1992; Louda et al. 1987; White 1978).

OCEANOGRAPHIC CONTEXT: PRODUCTIVITY AND RECRUITMENT

Recent studies suggest that, on relatively large spatial scales, nearshore oceanographic conditions may underpin significant differences in community impacts of individual species (Bustamante and Branch 1996; Bustamante, Branch, and Eekhout 1995; Bustamente, Branch, Eekhout, et al. 1995; Leonard et al. 1998; Menge 1992, 2000; Menge et al. 1997a, b, 1999). Variation in nearshore oceanography (nutrient concentrations, upwelling intensity, currents and mixing, phytoplankton blooms) can generate alongshore differences in phytoplankton productivity, rates of larval transport and delivery, and macrophyte production. Through bottom-up effects (e.g., nutrient and plant production impacts on food webs that "flow up" from the bottom of the web), such factors can alter communities both directly and indirectly through the modification of top-down effects. This latter effect is of particular interest, since it suggests a potential condition that might underlie variation in consumer-prey interaction strength and thus, perhaps, help explain the evolution of keystone species. In the follow-

ing pages, I present three examples that illustrate the importance of oceanographic context. I explore how oceanographic influences can govern variation in phytoplankton productivity, a bottom-up effect, and in turn how this may underlie the importance of top-down effects that are associated with predator species.

Example 1: Productivity and Prey Recruitment Effects in Oregon. Along the Oregon coast, phytoplankton concentration can vary dramatically on scales of 10s to 100s of km. Sampling initiated in 1993 has shown that phytoplankton concentrations (as estimated by chlorophyll-a concentration, hereafter termed chl-a) at Boiler Bay are consistently lower than those at Strawberry Hill (Menge et al. 1997a, b). This difference is particularly dramatic after summer upwelling events. Within 2–3 days of relaxation of an upwelling, chl-a reached concentrations greater than 30 µg/l at Strawberry Hill, while concentrations changed only slightly at Boiler Bay.

Associated with this difference were consistent differences in the growth rates of sessile filter feeders, including mussels and barnacles (Menge 1992; Menge et al. 1994; Sanford and Menge 2001). From 1990 to 2001, growth of the mussel *M. californianus* in annual transplant experiments has always been greater at Strawberry Hill. Similar measurements show comparable differences for the barnacles *Balanus glandula* and *Chthamalus dalli* (Menge 1992; Sanford and Menge 2001), and field observations suggest that the mussel *M. trossulus* also grows faster at Strawberry Hill.

What are the causes of these differences in growth rates of sessile filter feeders? Our initial hypothesis was that differences in growth rate were driven by between-site differences in phytoplankton concentration (Menge et al. 1997a). That is, mussels and barnacles grew faster because a likely major food source, phytoplankton and phytoplankton-derived detritus, frequently reached higher concentrations at Strawberry Hill. This explanation was not complete, however, because higher growth rates at Strawberry Hill appeared to be sustained during fall and winter, when phytoplankton blooms do not occur and detritus concentrations do not differ. A recent study confirmed these impressions (Sanford and Menge 2001). Quantification of growth rates of individual uncrowded barnacles showed that both *B. glandula* and *C. dalli* did indeed grow faster in response to phytoplankton blooms. The analysis also showed, however, that increased growth rates continued well beyond the period of high phytoplankton concentration. Further investigation suggested that faster barnacle growth was associated with two additional factors. First, since barnacles are known to consume invertebrate larvae (e.g., Navarrete and

Wieters 2000), it seemed possible that sustained growth after the cessation of blooms was due to the capture of zooplankton that were being transported past by currents. A comparison of short-term growth rates with recruitment data for barnacles during the same period was consistent with this notion. Moreover, recruitment of both barnacles and mussels at these sites has consistently been greatest during autumn months (September to December; B. Menge, unpubl. data). Thus, if zooplankton are in fact an important food source for filter feeders, the apparently high growth rates of filter feeders sustained through fall and winter may be a direct consequence of higher rates of onshore transport of zooplankton.

Second, a spurt in growth in late summer and early fall may also be influenced by a more favorable thermal regime. Water temperatures during summer often fall below 10°C due to upwelling events, which largely cease in September. As a consequence, temperatures tend to stabilize at around 12–14°C, gradually falling to about 10°C in winter (Sanford 1999a; B. Menge unpub. data). In contrast, air temperatures experienced by barnacles in the intertidal region tend to decline as summer gives way to fall because of seasonal changes and because lower low tides shift from daylight (morning) to nighttime in October. Because more moderate temperatures foster greater efficiency in the conversion of food to growth and reproduction, increased growth in autumn may also reflect a more favorable thermal regime.

What are the potential factors underlying the differential onshore transport of larvae and particulate food for filter feeders? Elsewhere (Menge et al. 1997a), evidence suggested that differing nearshore oceanographic conditions might lead to the dilution of plankton offshore from some coastal sites (e.g., Boiler Bay) and the concentration of plankton offshore from others (e.g., Strawberry Hill). Satellite imagery and coastal surveys of phytoplankton concentration suggested that the variable width of the continental shelf was associated with an uneven pattern of current flow nearshore that might tend to transport plankton away from the coast at Boiler Bay and concentrate plankton in a gyre adjacent to Strawberry Hill. Recent quantification of surface currents using high-frequency radar (which quantifies surface currents with resolution of about 2 km) is consistent with this hypothesis. Currents during upwelling tend to be strongly offshore toward the southwest off Boiler Bay and weak and variable off Strawberry Hill (M. Kosro, unpub. data). Assuming that the surface currents reflect patterns of the movement of larvae, such physical patterns would lead to low residence times for propagules and detrital particulates in waters off Boiler Bay but high residence times for particulates in waters off Strawberry Hill. Further research is necessary to sort out the

relative influences of phytoplankton and particulate concentration, larval condition, other meroplankton (larvae of benthic species) food sources, and thermal regime as determinants of the higher growth of filter feeders in rocky intertidal regions.

In summary, the evidence that oceanographic processes drive between-site differences in prey productivity—a bottom-up process—is strong. Do such differences influence top-down processes as well? The mussel transplant experiments used to test predation rates (summarized earlier) suggest that they do. In three separate experiments, two using *M. californianus* and one using *M. trossulus* (Menge 2000; Menge et al. 1994; Navarrete and Menge 1996), predation (per population) rates were always greater at Strawberry Hill, and were generally greater at wave-exposed areas than at wave-protected areas. Longer-term (approximately 3-yr) removal of *Pisaster* led to changes similar to those seen by Paine (1966, 1974): the lower edge of the mussel bed migrated downward, presumably due to the lack of sea stars "browsing" on mussels that were pushed downward by lateral pressure from growth, and to the recruitment of mussels within the bed.

In a separate experiment that tested the impact of predation, predators (primarily *Pisaster*) were excluded using standard caging techniques in the low zone in wave-exposed and wave-protected areas at each site (fig. 2.2). All experiments began with surfaces free of sessile biota (scraped but not sterilized) in July 1989 and ran until August 1990. Results showed that in the presence of predators, the barnacle *C. dalli* settled and grew to persist as the dominant space occupant at both sites, ranging in final cover from about 30% to about 70%.

In the absence of predators, results differed between sites. At Boiler Bay, *C. dalli* was generally the most abundant sessile organism, although both *B. glandula* and *M. trossulus* were present in low abundance. In contrast, at Strawberry Hill, mussels (*M. trossulus*) recruited rapidly to the cages, overgrowing and displacing the barnacles. Mussels also became abundant over the winter in +predator treatments at the wave-exposed site at Strawberry Hill but were eaten by July of the following summer (see fig. 2.2G, H). The apparent between-site difference in predator impact in this experiment (see fig. 2.2) is most simply interpreted as a difference in the rate at which mussels colonized cages. Thus, the results of the mussel transplant experiments appear to provide a clearer picture than do cage experiments of the actual predation regimes at each site, even though the results in both transplant and cage experiments superficially led to similar interpretations (i.e., predation is more intense at Strawberry Hill).

A final feature of community dynamics at these sites is that population densities of *Pisaster ochraceus* are higher at Strawberry Hill than

at Boiler Bay and are also much more abundant at wave-exposed sites than at wave-protected sites (Menge et al. 1994). As also observed on Vancouver Island (Robles et al. 1995), *Pisaster* respond quickly to changes in prey concentration, forming large feeding aggregations that often consisted of hundreds of individuals. These aggregations are common in the low zone at Strawberry Hill (Sanford 1999a, b; B. Menge pers. obs.). Mussel patches developing over winter are usually surrounded by sea stars by spring and eliminated by mid-summer. Thus, dense concentrations of prey may affect the abundance of sea stars at least on short-term and local scales, through a numerical response. It seems reasonable to suggest that longer-term, larger-scale variation in sea star abundance is also a function of consistent between-site differences in prey populations, such as those documented at Boiler Bay and Strawberry Hill.
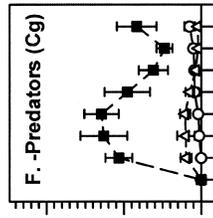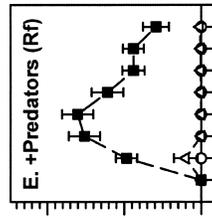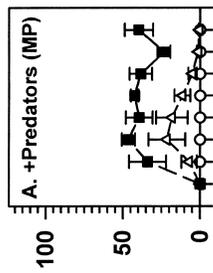
Another factor that could affect sea star abundance is recruitment. Although quantitative estimates suggest that the recruitment of sea stars may be somewhat higher overall at Strawberry Hill, differences were not large, and monthly peaks of recruitment were sometimes higher at Strawberry Hill and sometimes higher at Boiler Bay. Further, size structure (g of wet mass) samples indicated that juveniles (≤ 50 g wet mass) were actually proportionately more abundant at Boiler Bay (Menge et al. 1994). I conclude that between-site recruitment differences are unlikely to explain the differences in sea star abundance or effect.

Collectively, these results suggest that two environmental characteristics—recruitment and secondary production of prey—drive between-site differences in predation regime. In other words, more intense predation is associated with higher rates of prey production. In this case at least, variation in bottom-up processes can therefore underlie differences in top-down effects. Thus, the community impact of the keystone predator *Pisaster ochraceus* seems at least partly dependent on the oceanographic context.

Example 2: Prey Productivity and Recruitment Effects in New Zealand. In general, the rocky intertidal region of the South Island of New Zealand has typical patterns of community structure (Knox 1953; Menge et al. 1999). High, middle, and low zones are dominated by barnacles, mussels, and macrophytes, respectively. Patterns on the east coast contrast sharply with those on the west coast, however. At sites on Banks Peninsula on the east coast, mussels (*Mytilus galloprovincialis*, *Perna canaliculus*) dominate the middle and low zones, often ranging down to the upper edge of the infralittoral zone, abutting a zone of the massive brown macrophytes *Durvillea willana* and *D. antarctica*.
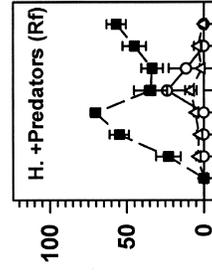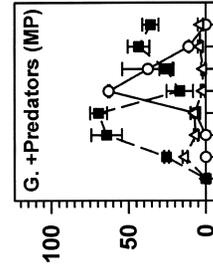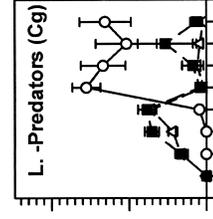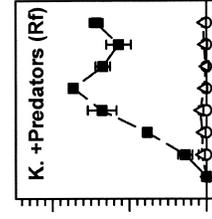
Boiler Bay

Strawberry Hill

Exposed

Protected

Exposed

Protected

A. +Predators (MP)

D. +Predators (MP)

G. +Predators (MP)

J. +Predators (MP)

B. +Predators (Rf)

E. +Predators (Rf)

H. +Predators (Rf)

K. +Predators (Rf)

C. -Predators (Cg)

F. -Predators (Cg)

I. -Predators (Cg)
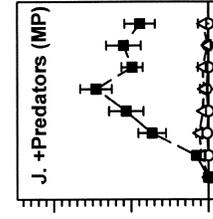
L. -Predators (Cg)

Percent Cover

7/15 9/1 10/14 11/15 4/27 6/22 7/22 8/21

--△-- *Balanus glandula*   —■— *Chthamalus dalli*   —○— *Mytilus trossulus*

Predators (e.g., the whelk *Thais orbita* and sea stars *Coscinasterias calamaria* and *Stichaster australis*), though present, are scarce. In contrast, while mussels dominate the middle zone at sites on the central west coast, the low zone consists of free space (bare rock and algal crusts) on the upper portion and red algal turf (mostly mixed *Champia* sp. and *Gigartina* spp.) on the lower portion. Predators (mostly *S. australis* but also *T. orbita* at some sites) are abundant.

The northern half of the west coast lies in a region of intermittent upwelling. On colliding with the west coast, the southeastward-flowing Tasman current separates into the northeastward-flowing West-land current and the southwestward-flowing Southland current (Menge et al. 1999; Neale and Nelson 1998). These conditions, and summer orographic effects, cause intermittent upwelling along the northwest coast. The remainder of the west coast as well as the south and east coasts lie in a downwelling region of the Southland current, which wraps around the island (Vincent et al. 1991).

Studies that quantify key community processes and environmental conditions (predation rate, grazing effects, recruitment, mussel growth, air and sea temperature, wave forces) were conducted at sites on the east and west coasts to test the prediction that both bottom-up and top-down forces would be greater in the west coast upwelling ecosystem. Briefly, results were consistent with these predictions. Predation was more intense on the west coast than on the east coast. In particular, the sea star *Stichaster australis* had a powerful influence on community structure; sea stars removed most transplanted mussels within 2 to 3 months. Further, in the absence of this sea star, mussel abundance increased steadily in cover (mostly by recruitment and growth), occupying 20–30% of the previously bare low zone in only 6 months. With Paine's (1971) studies on the west coast of the North Island of New Zealand, these results suggest that this sea star is a keystone species.

Mussel and barnacle recruitment rates were also in general orders of magnitude greater, and mussel growth, as indexed by RNA:DNA

Figure 2.2 Consequences of exclusion of *Pisaster ochraceus* and whelks (*Nucella ostrina, N. canaliculata*) on sessile prey abundance (% cover, estimated from photographs using random-dot methods) at wave-exposed and wave-protected areas at Boiler Bay and Strawberry Hill from 1989–1990. Treatments were marked plot (MP; +predators), roof (Rf; +predators), and cage (Cg; −predators). Both predation impact and the rate of colonization by mussels were greater at Strawberry Hill than at Boiler Bay.

ratios (Dahlhoff and Menge 1996; Menge et al. 1999), appeared greater on the west coast as well. Temperature patterns of the seawater exhibited clear upwelling-characteristic trends on the west coast (periodic sharp drops of 3–4°C, with rapid recovery after days to a week or more) and downwelling-characteristic trends on the east coast (mostly steady trends with only slight temperature fluctuations). Limited nutrient samples suggested that upwelling generated elevated nutrient levels on the west coast while east coast nutrient concentrations were consistently low. Dynamometer data suggested that wave forces were similar at both sites (Menge et al. 1999).

Although nearshore oceanographic conditions remain only sketchily known in New Zealand, these results, occurring on a biogeographic scale in contrasting oceanic regimes (upwelling vs. downwelling) are consistent with the Oregon studies, which were conducted on smaller spatial scales within an upwelling regime. Stronger bottom-up effects were associated with stronger top-down processes. Thus, oceanographic context may be critically important in determining patterns of rocky intertidal community structure and dynamics. As in the northeast Pacific, keystone predation in these New Zealand sites was associated with an upwelling ecosystem.

Example 3: Nutrient and Kelp Inputs in South Africa. A final example of strong oceanographic effects on rocky intertidal community structure offers interesting contrasts as well as similarities to the results in Oregon and New Zealand. Around the South African coast, upwelling is strong on the west, less on the south, and weak on the east (Bustamante, Branch, Eekhout, et al. 1995b). Nutrient concentrations and estimates of benthic algal productivity are correlated positively with these oceanographic changes, as are grazer biomass and filter-feeder biomass. Field experiments suggest that grazer biomass is strongly related to the rate of delivery of macrophyte detritus from nearshore kelp stands (Bustamante, Branch, Eekhout, et al. 1995a), and thus, by extension, that the correlation between benthic algal productivity and grazer biomass is driven by nearshore oceanographic conditions. Grazing impacts by the limpets on resident macrophytes were high where productivity was highest and lower where productivity was low.

Unlike most other coasts in upwelling regions, however, the South African rocky intertidal ecosystem evidently does not harbor a dominant keystone predator, such as the sea stars or whelks discussed earlier (R. Paine pers. comm.; G. Branch pers. comm.). Under some circumstances, oystercatchers (*Haematopus moquini*) can decimate limpet abundance, leading to increases in algal cover (Bosman et al.

1986; Bosman and Hockey 1986; Branch et al. 1987). These dynamics tend to be localized in regions that have high inputs of guano and where oystercatchers are not regarded as keystone predators. Thus, in the Benguela upwelling ecosystem, no keystone predator has evolved that exhibits a community function parallel to those seen in the northeast Pacific, the west coast of New Zealand, or the central Chilean coast (Duran and Castilla 1989; see later, under *Potential for Compensation*). Whether this exception offers further insight into the evolution of keystone species awaits further research.

Biotic Context

As noted earlier, the biotic context of a species includes community diversity, particulars of species composition, and characteristics of key interactors. Another factor, the rate of resource replenishment (e.g., recruitment and growth), was considered from a large-scale oceanographic perspective. Aspects of recruitment effects can be considered an important component of biotic context as well, as I discuss in this section. As in other sections, I restrict myself largely to studies of consumer-resource interactions and concentrate on examples taken from my own research activities.

POTENTIAL FOR COMPENSATION
Community diversity can dictate the response to the loss of a species by regulating the remaining species' role in compensating for the lost interactor's effect. Such responses can be key determinants of the persistence and adjustment stability of a community (e.g., Sutherland 1974). For example, in some New England middle and high zones, the absence of predators other than *Nucella* probably means that wholesale changes in community structure would occur if this whelk were to disappear from the ecosystem. Experiments reported earlier suggest that under this scenario, mussels would become the dominant occupants of midzone space in areas of intermediate wave exposure and perhaps even in sheltered rocky habitats (but see Bertness et al. 1999). Judging from the results of small-scale caging experiments, this change would probably lead to a greatly reduced abundance of fucoids because mussels, when dense, can trap algal fronds with their byssal threads and smother them (Menge 1976).

The widespread loss of such an important community component is not far-fetched. Studies in Great Britain in the 1980s revealed that TBT (tri-butyl tin), a chemical used as an antifouling agent, led to sterilization of female whelks, ultimately leading to sharply reduced

population sizes (Bryan et al. 1986). The effect of TBT was observed on rocky shores outside of boat harbors and was geographically widespread. I am unaware of studies of the community impact of this loss, but the similarities between New England and Great Britain communities suggest that large increases in mussel cover on rocky shores are likely. This prediction could be tested readily.

In Chile, harvesting by humans has drastically reduced the abundance of a large whelk, *Concholepas concholepas*, with dramatic consequences to the community (Castilla and Duran 1985; Duran and Castilla 1989). At this site, Mussels (*Perumytilus purpuratus*), normally limited to a narrow band high on the shore, spread downward and reduced the abundance of a variety of algal and herbivore species. In this case, alternative predator species (sea stars *Stichaster striatus*, *Heliaster helianthus*) co-occurred within the system. Separate experiments suggested that these sea stars could maintain significantly lower mussel densities than occurred in their absence, suggesting that there exists some potential for compensation (Paine et al. 1985). Sea star effects were not of the same magnitude as those of the whelk (compare Paine et al. 1985 with Duran and Castilla 1989), however, suggesting that in this system the sea stars were relatively weak interactors. Further study would be necessary to test this inference.

Although much evidence suggests that keystone species occur in many communities and in all habitat types (Power et al. 1996b), few studies have explicitly tested the keystone species hypothesis (Menge et al. 1994; Menge and Freidenburg 2001). If the deletion of a single species results in a large change in the community, the inference that the species is a keystone species is robust, because the change occurred despite the presence of other consumers in the community (Paine 1966, 1971, 1974). However, the deletion of a putative keystone species with no resulting change does not mean that a keystone species is not present, since the experimenter might have chosen the wrong species. To test keystone predation rigorously, the experimental design should include treatments that remove all individual potential keystone species as well as separate treatments that involve the removal of all consumers.

As in the rocky intertidal system studied by Paine on the outer Washington coast, communities on the Oregon coast include a diverse guild of predators, including *Pisaster ochraceus* and several species of whelks (*Nucella ostrina, N. canaliculata, and Searlesia dira*). The abundance of these predators can vary strikingly among sites (see earlier for data on *Pisaster*). Paine's *Pisaster* removal experiments clearly implied that, in terms of community impact, whelk predation at his sites was weak. Other studies in the same and in other systems, however,

suggest that whelks can be strong interactors with large community effects (Connell 1970; Dayton 1971; Luckens 1975; Menge 1976; Duran and Castilla 1989; Fairweather and Underwood 1991). These studies and extraordinarily high densities of whelks at Strawberry Hill on the Oregon coast suggest that under some conditions, whelks might be strong interactors in the low zone (Navarrete and Menge 1996).

To test this possibility in the context of keystone predation by *Pisaster*, we quantified the survival of transplanted *M. trossulus* in all combinations of *Pisaster* and *Nucella* species' presence and absence. Experiments were established at wave-exposed and wave-protected areas at sites of naturally low and high predator density (Boiler Bay and Strawberry Hill, respectively). Results indicated that, as expected, *Pisaster* had an overwhelmingly powerful impact on mussel survival whether or not whelks were present. In the absence of *Pisaster*, however, whelk impacts were surprisingly strong, although still less than that of the sea star. These effects were largely a consequence of high population densities of whelks; the per capita, interaction strength of sea stars was 2–3 orders of magnitude greater than that of whelks. Thus, although *Pisaster* was unquestionably a far stronger interactor, the normally weakly interacting whelks still have the potential to compensate partially for the loss of sea stars with a increased impact on prey populations.

EFFECTS OF SPECIES COMPOSITION
Another example from New England suggests that the resilience of other portions of the rocky intertidal zone could be much greater than that suggested for the middle zones. In the low zone at sites of intermediate and low wave exposure, several other predator species join whelks as predators (see earlier, under *Environmental Conditions*, and Menge 1983). Caging experiments that were used to test the total impact of predation on this community (Lubchenco and Menge 1978) showed that mussels (*M. edulis*) eliminated red algal turfs, the normal dominant species at intermediate and sheltered areas. But which predators were responsible for this effect? By combining the feeding rates of each species observed in field experiments with rates of mussel recruitment and predator densities, I could estimate the relative contribution of each species to the predation regime (Menge 1983). These calculations suggested that although one or two species tended to be the dominant predator at each site, the actual dominant varied among sites (fig. 2.3). The crab *Carcinus maenas* was evidently the most important predator at Canoe Beach Cove, for example, while sea stars (*Asterias vulgaris* and *A. forbesi*) were most important at Chamberlain, and whelks dominated at Grindstone Neck. The clear implication is
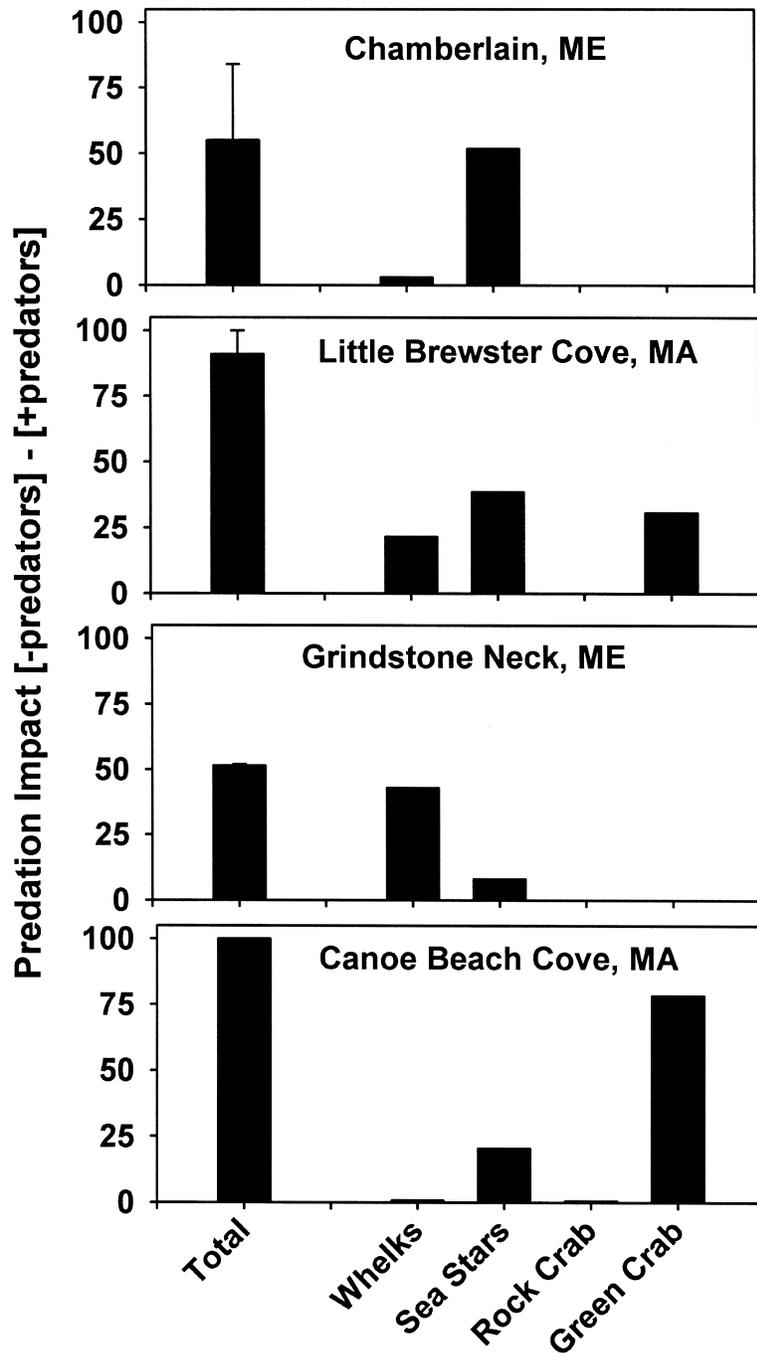
that in the low zone, predation is generally strong but that the species responsible for this impact varies in space. Further, the community is likely to be resilient to the loss of one or two consumers from this guild. Hence, in a diverse predator guild, compensatory tradeoffs among species may buffer the consequences of species losses in the low zone.

A final example comes from the rocky shores of the Pacific coast of Panama, where community diversity is very high. The results from this site further exemplify the buffering effects of a diverse guild of consumers. Compared to the temperate rocky intertidal communities, the rocky shores along the tropical east Pacific coast are nearly barren of sessile organisms. Barnacles, mussels, and oysters are sparse, and macrophytes are very small (generally <2 cm in thallus length) and limited mostly to thin turfs in the low zone (Lubchenco et al. 1984; Menge and Lubchenco 1981). Mobile invertebrates are relatively abundant but are largely hidden away in crevices and holes. The exceptions are grazing gastropods (neritids), which cluster in the high zone, and limpet species (*Siphonaria* spp., *Fissurella* spp.), which home to scars on open rock surfaces of the mid zone. In this system, the types of consumers (crabs, fish, whelks, sea stars) and the number of species per type were diverse (Lubchenco et al. 1984; Menge et al. 1986b). Patterns of space occupancy and zonation in this community appeared relatively constant. During 7 years of investigation, the only observed changes in community structure were brief and slight increases in the cover of ephemeral green algae during the early part of the dry season (December–January) (Lubchenco et al. 1984).

The high diversity of consumers in this community sharply con-

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Figure 2.3 Consequences of the exclusion of predators at Chamberlain, ME; Little Brewster Cove, MA; Grindstone Neck, ME; and Canoe Beach Cove, MA; with estimates of per-species effects. Total predation effects were estimated as the final difference in percent cover of mussels in +predator (marked plots, roofs) and −predator (cages) treatments (see Lubchenco and Menge 1978). The effects of whelks (*Nucella lapillus*), sea stars (*Asterias vulgaris* at Grindstone Neck; *A. vulgaris* and *A. forbesi* at the other sites), rock crabs (*Cancer borealis*), and green crabs (*Carcinus maenas*) were determined using estimates of feeding rates on mussels (*Mytilus edulis*) in field cage experiments, field predator and prey densities, and mussel recruitment rates quantified using collectors (10-cm × 10-cm pieces of shag rug glued to marine plywood; see Menge 1983). Predation was generally strong at all sites, but different predators or sets of predators varied in importance among sites. Potential compensation for the loss of a predator species should be high in such a community.

strained the design of experiments that tested the effects of predation. Because the removal of individual species would have generated an impossibly large number of treatments, not to mention experimental units, we focused on the exclusion of species in four types of consumers. These were slow-moving grazers (mostly limpets and chitons), slow-moving predators (mostly whelks), fast-moving large fishes (mostly omnivorous consumers of sessile biota), and fast-moving small, benthic consumers (crabs and fishes such as blennies). Using an orthogonal design would have yielded 16 treatments. Despite this simplified design, however, it was impossible to delete the small fishes and crabs while allowing large fishes to enter the plots, so the final design was limited to a (still daunting) 12 treatments in each of three zones: high, middle, and low (Menge and Lubchenco 1981; Menge et al. 1986a).

These experiments suggested that in this community, predation was strong but was a cumulative effect of several consumers. The cover of sessile biota increased in the absence of consumers, but the largest increase, by far, was observed only in the total absence of consumers (Menge et al. 1986a). Further, the exposure of dense prey concentrations to consumers revealed that predation was intense; within hours to weeks, even well-defended prey were decimated (Menge et al. 1986b).

In Panama, the predation regime was evidently not characterized by a single, or even two or three, strongly interacting species, but by a minimum of four and most likely more consumers. Although by manipulating the consumer groups, we were removing many species and not just one in each treatment, each group was numerically dominated by two to three species (Lubchenco et al. 1984). This predation regime, now termed "diffuse" predation (Hixon 1991; Robles and Robb 1993; Menge et al. 1994), seems to consist of a group of consumers whose effects are additive rather than nonlinear, as would be expected if a keystone predator were present. By itself, each group had a small contribution to total predation (fig. 2.4), and this effect was not detected readily in the treatments involving the removal of only a single group (Menge et al. 1986a). Only by averaging across treatments (i.e., removals of one, two, and three species) differing by the presence or absence of a particular group was the effect in figure 2.4 detectable.

Although strictly speaking, these experiments do not reveal the role of individual species, our results suggest that the highly persistent structure of this community is dependent on a taxonomically and functionally diverse array of consumers. Judging by their abundance, size, and foraging patterns, dominant consumers in this assemblage
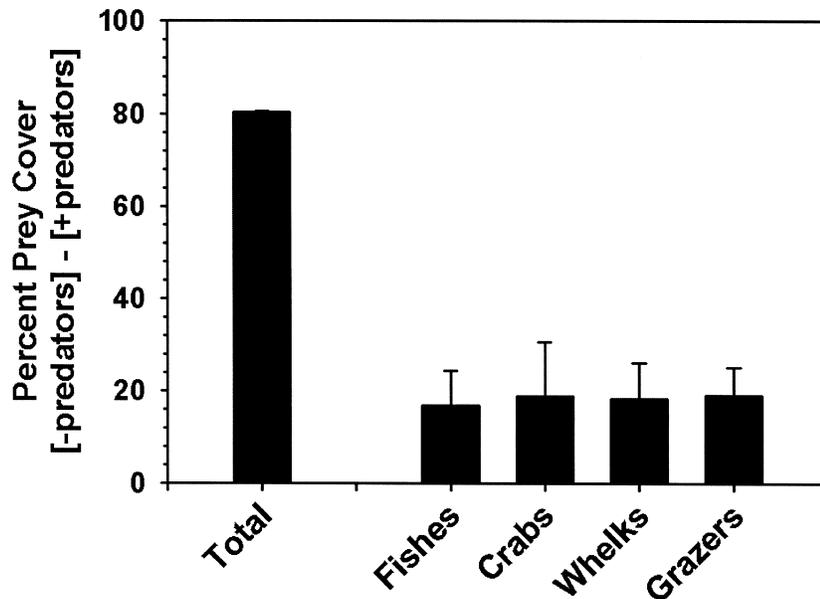
Figure 2.4 Effect of consumers, collectively and by each of four single groups (fishes, F; crabs, C; whelks, W; molluscan grazers, G) on total prey abundance in the rocky intertidal region at Taboguilla Island, Panama. Prey included sessile invertebrates (mostly barnacles and bivalves), colonial invertebrates (hydrozoans), and algae. The estimate of the effect of consumers was based on the % cover of prey in the absence and presence of all consumers (total) and each group separately. Single-group effects were estimated by determining the difference between treatments that differed in whether the particular group was included in the treatment. For example, fish effects were estimated by treatments $+F+C+W+G$ vs. $-F+C+W+G$, $+F+C-W+G$ vs. $-F+C-W+G$, etc. Error bars are 1 SE. Predation was strong but diffuse in this community, which should be highly resilient to the loss of predator species. Data from Menge et al. (1986a), after Menge and Freidenburg (2001).

included the porcupinefish (*Diodon hystrix*), a wrasse (*Bodianus diplotaenia*), a parrotfish (*Scarus perrico*), a damselfish (*Stegastes* sp.), a predaceous crab (*Ozius verreauxii*), three whelks (*Acanthina brevidentata, Purpura pansa, Thais melones*) three limpets (*Fissurella virescens, F. longifissa, Siphonaria gigas*), a chiton (*Chiton stokesi*), and an omnivorous crab (*Grapsus grapsus*). The great diversity of trophic apparatus included in this heterogeneous group is undoubtedly an important factor in holding a diverse group of prey populations at consistently low abundance. The results of this experiment also suggest that the community was

highly resilient to species losses. Presumably due to compensatory changes—such as speedy aggregation to concentrations of prey, shifts in prey preference, and population increases—consumer species in this assemblage were able to suppress fluctuations in prey rather quickly.

EFFECT OF SPECIES CHARACTERISTICS

A crucial but still unresolved issue in community ecology is determining what factors underlie the interaction strength between consumers and prey. In particular, understanding the ecological and evolutionary conditions that generate keystone species is an important but unsolved problem (Menge et al. 1994; Menge and Freidenburg 2001). Although a variety of species traits and ecological conditions have been proposed as possible explanations, and some of these are undoubtedly important, the evidence remains equivocal. In rocky intertidal communities at least, four factors stand out as potentially critical characteristics: (1) the presence of a strong, competitively dominant space occupier, (2) a consumer that preys disproportionately on the competitive dominant, (3) relatively large sizes of these critical species, and (4) high prey production. As noted elsewhere (Menge et al. 1994; Menge and Freidenburg 2001), the first two traits seem to be associated with strong predation systems in general, not just keystone-dominated systems. There are also apparent exceptions to the second two traits. If whelks can be considered keystone predators in some systems (e.g., Menge 1976, Duran and Castilla 1989), they are not always large relative to competitively dominant prey species (e.g., on New England rocky shores).

Some evidence suggests that systems that have keystones are located in upwelling ecosystems with high rates of nearshore productivity, prey recruitment, and prey growth (northeast Pacific, west coast of New Zealand, central coast of Chile). However, as noted earlier, the highly productive Benguela Current ecosystem on the west coast of South Africa is a glaring exception (R. Paine, G. Branch pers. comm.). Here, evidently, there is no strongly interacting intertidal predator. Further study may reveal the special circumstances that have generated such different community dynamics, but for the moment it seems clear that an understanding of some crucial part of the puzzle that leads to the evolution of keystones is still lacking.

Discussion

Understanding, and ultimately predicting the likely consequences of species loss seems critically dependent on understanding how the

abiotic and biotic environmental contexts shape species interactions. In this sense, I argue that environmental context is the overridingly important determinant of a species' impact. To what extent can we predict the consequences of species deletion based on present knowledge?

The consequences of abiotic stress seem clear, at least for invertebrate predators on rocky shores. Under conditions of high thermal stress, desiccation stress, or high hydrodynamic forces, the community impact of predators is likely to be diminished. With respect to abiotic stress, however, at least two issues remain to be resolved. First, at the level of herbivore-plant interactions, heightened stress can increase rather than decrease consumer impacts (Menge and Olson 1990; Louda and Collinge 1992; Olson 1992; B. Menge and A. Olson unpub. data). The basis for this is not yet clear, but it depends in part on size differences among plants and herbivores as well as the greater susceptibility of certain plants to thermal and desiccation stress relative to their consumers. Although these trends have been apparent for some time, progress in understanding them has lagged and further research would be rewarding.

Second, the quantification of stress effects on living organisms has, until recently, been stymied by the lack of appropriate techniques for detecting stress. Mass mortality is readily observable but helps little in quantifying the impact of abiotic stress in the context of species interactions. Promising new tools developed by molecular physiologists, however, may spur progress on the issue of detecting and quantifying sublethal stress, how this varies under varying abiotic (including oceanographic) conditions, and its ecological consequences. Methods of determining levels of heat-shock proteins (HSPs) and RNA:DNA ratios, for example, provide relatively quick and inexpensive ways of quantifying the impacts of thermal stress and short-term growth responses to food availability, respectively (Hofmann and Somero 1995, 1996a, b; Dahlhoff and Menge 1996; Roberts et al. 1997). Combining these methods of quantification with field experiments that test species interactions under conditions of different levels of stress (e.g., Dahlhoff et al. 2001; J. Burnaford unpub. data) will likely fuel dramatic advances in the understanding of the roles of variation in stress and food levels.

The consequences of varying oceanographic conditions may also be predictable. The studies of rocky intertidal communities in upwelling ecosystems summarized earlier suggest that communities typified by strong top-down species interactions occur where bottom-up processes—specifically, rates of larval delivery and phytoplankton productivity—are high. In Oregon and along the west coast of New Zealand's South Island, high recruitment and growth dynamics of prey

populations seemed fueled by oceanographic conditions that favor the retention of nearshore plankton and the delivery of plankton concentrations to intertidal areas on a frequent basis. High rates of such bottom-up effects seem to underlie strong top-down effects and, with some as-yet unknown condition or process, may underlie keystone species–dominated ecosystems.

Further Observations: New Zealand

Comparisons between the west and east coasts of the South Island of New Zealand, and between different sections of the California current ecosystem offer further insight. As summarized earlier, at sites in New Zealand, bottom-up processes were low on the East Coast, an apparent downwelling-dominated ecosystem, and high on the West Coast, an area of intermittent upwelling (Menge et al. 1999). The hypothesized consequence of this difference was strong top-down effects on the west coast and weak top-down effects on the east coast. Preliminary observations during ongoing studies examining the impact of nearshore oceanography suggest that, as predicted, onshore community structure and dynamics vary strikingly as a function of oceanic conditions (B. Menge et al. unpub. data). Communities occurring in downwelling conditions have few carnivores and sparse to near-absent populations of filter-feeding invertebrates. Observations at a total of six sites around the South Island indicate that zonation patterns at some sites are difficult to discern, both because zone-forming invertebrates (mussels and barnacles) are sparse to absent, and because the sharp zone boundaries imposed in other ecosystems by competition or predation are diffuse. Recruitment rates appear very low as well. Only grazers do well on the east coast; high densities of grazers (limpets, chitons, coiled gastropods) occur at all sites. Although dense stands of *Durvillea* spp. and red algal turf occur in low zones, macrophytes are sparse to absent in the middle and high zones from wave-exposed New Zealand rocky intertidal communities. These communities (near Kaikoura, Christchurch, and Dunedin on northeast, central, and southeast parts of the east coast) contrast strongly with two sites in the northwest upwelling region of the South Island. At these west coast sites, communities are vibrant: filter feeders are dense, grow fast, recruit at high densities; carnivores are abundant and large; and predation is strong (B. Menge et al. unpub. data).

A site on the southwest coast, Jackson Head, near Haast, appears intermediate between the communities in the upwelling zone to the north and the east coast sites. Here the two mid- and low-zone mussels (*Perna*, *M. galloprovincialis*) are absent, but a small high-zone mus-

sel *Xenostrobus pulex* is abundant. Barnacles (*Chamaesipho columna*, *Epopella plicata*) dominate space in the high and middle zones. Sea stars and whelks (*T. orbita*) are common but less abundant than at the northern upwelling-influenced sites. Preliminary evidence suggests that the recruitment of mussels and barnacles is intermediate between the high rates that occur in the upwelling region and the low rates seen on the east coast.

These observations and our earlier studies are consistent with the notion that oceanographic conditions can predict patterns of rocky intertidal community structure and dynamics. As expected, mussel and barnacle recruitment rates evidently decline with distance from the upwelling region on the west coast of the South Island. A reduced abundance of adult filter feeders at the southwest, southeast, and northeast sites is consistent with the hypothesis that larval transport (for these species, at least) is low in downwelling ecosystems. The central east coast site, Godley Head on Banks Peninsula, with high barnacle and mussel covers, is an apparent exception to this trend. However, the northward-flowing Southland current is in the lee of the Banks Peninsula, which may generate larvae-concentrating eddies and relatively high subsequent recruitment rates. These possibilities are currently under investigation.

Looking to the Future

In asking whether the effects of species loss could be predicted, I have described in some detail the results of much of my own research, in which the context of species interactions exerts an overriding influence on the expected impact of a species loss. A danger in my approach, however, is that the reader may get lost in the detail and miss my attempt to outline a framework for predicting consequences of species extinction. My point is that predicting responses to species loss depends on the context (hence the detail) but that certain principles guide how context should be defined. Key features of context are environmental influences (e.g., productivity and physical stress) and, to some extent at least, the responses to species loss along gradients of these influences is predictable.

In attempting to make predictions about species loss, it is clear that a large-scale, long-term perspective that goes well beyond particular species interactions is needed. Using such a perspective will be hard work, and predictions will need to be explored in terrestrial and freshwater as well as marine habitats. To succeed, such endeavors will require new funding, new research partnerships, and the adoption of creative new approaches to the integrative study of ecosystem

dynamics. Then will also require a stronger sense of cooperation among scientists that have the expertise required to investigate problems on large scales that necessarily cross disciplinary boundaries. Ecologists will need to incorporate new technologies and methodologies into their research ventures. An understanding of the mechanisms that underlie the phenomena that occur on larger or longer scales will require the use of techniques and technologies that are both under development and in use in fields as diverse as landscape ecology, physical and chemical oceanography, remote sensing, physiology, molecular biology, and genetics. Although it is impossible to forecast the level of precision that might be achieved in predicting the consequences of species loss, I am optimistic that dramatic strides in predictive capacity will be made over the next decade.

As witnessed by his scientific legacy, which is at least partly reflected in the articles in this volume, Bob Paine has had a profound impact on ecology. Many of the consequences of species loss, for example, were first revealed by his experiments. These ecological insights attracted attention, and his energy and charisma attracted many students and colleagues eager to participate in the excitement and ferment of his laboratory. Inevitably, many of these students, postdocs, collaborators, and colleagues have also contributed substantially to the ideas and details of ecological systems.

Above all, we were encouraged by Bob to be naturalists—to let nature guide us in our probing and prodding and hopefully provoke us to ask questions that would reveal the innermost secrets of the workings of natural systems. For many, the thrill of such activities came in large part from having solved a puzzle—from satisfying one's curiosity and learning how nature works. These days, of course, nature is reeling, suffering from the tsunami of humanity and its many negative effects, including massive species loss. Many of us hope that the knowledge fostered by Bob and his associates will contribute to efforts to reduce these insults to the Earth. Although humanity has, to date, lacked the political will to take serious action to stem the onslaught, I remain cautiously optimistic that grassroots efforts and our growing scientific awareness will force a global adoption of strong and appropriate measures, and that we can at least slow the growing tide of species loss.

Acknowledgments

three reviewers, on the manuscript. By taking a chance on a naïve Minnesotan with no understanding of how science was done, Bob Paine provided me with a priceless opportunity and a major redirection of my life. I hope that, in a small way at least, my contributions to scientific progress have justified his decision and his ongoing support throughout my career. Much of the work and insights I summarized in this paper was also influenced by collaborations with students and colleagues. In particular, I thank my mate and research partner Jane Lubchenco for her help, support, and tough critiques throughout my career. Colleagues and former students deserving particular mention for their important insights into community dynamics include Gary Allison, Eric Berlow, Elizabeth Dahlhoff, Steve Gaines, Brian Grantham, Patti Halpin, Mark Hixon, Gretchen Hofmann, Sergio Navarrete, Karina Nielsen, Annette Olson, Eric Sanford, George Somero, Ted Strub, and Pat Wheeler. I thank all those in the "Lubmengo" group for their never-ending efforts to keep me humble and young in mind, if not body. This chapter is contribution number 19 from PISCO, the Partnership for Interdisciplinary Studies of Coastal Oceans, a Long-Term Ecological Consortium funded by a grant from the David and Lucile Packard Foundation. My research has been supported by grants from the National Science Foundation, the Andrew Mellon Foundation, a John Simon Guggenheim Fellowship, an endowed professorship from the Wayne and Gladys Valley Foundation, and the David and Lucile Packard Foundation.