

Ecosystem effects of fishing in kelp forest communities

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Kelp forests, highly diverse cold water communities organized around the primary productivity and physical structure provided by members of the Laminariales, support a variety of fisheries, and the kelp itself is harvested for alginates. Worldwide, these communities generally share susceptibility to destructive overgrazing by sea urchins. The impact of sea-urchin grazing is governed by the ratio between food availability and grazing pressure, thus factors affecting the abundance of both urchins and kelps are central to ecosystem integrity. Some kelp ecosystems share a second generality, the association of exploitation of various urchin predators with destructive levels of urchin grazing, leading to cascading implications for other species dependent on the productivity and habitat provided by the kelps. Competition between abalones and sea urchins also affects some kelp communities. These ecosystem-structuring processes are complicated by a variety of bottom-up and top-down factors, including variability in ocean climate affecting kelp productivity and recruitment of key species, and echinoid disease. Potential ecosystem effects of fisheries for predators, abalones, sea urchins, and kelps are reviewed biogeographically. Given the hundreds to thousands of years that many nearshore marine ecosystems have been exploited, no-take marine reserves may be the only way to determine the true ecosystem effects of fishing.

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Key words: abalones, exploitation, kelp harvest, predators, sea otters, sea urchins, urchin disease.

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Introduction

Kelp forests are shallow coastal communities of cold-water regions organized around the structure and productivity provided by members of the Laminariales (reviewed by Mann, 1982; Dayton, 1985a). These large algae are adapted to vigorous water movement and turbulent diffusion that allows very high levels of nutrient uptake, photosynthesis, and growth. The productivity of kelp forests rivals that of the most productive terrestrial systems, with up to $3 \text{ kg C m}^{-2} \text{ yr}^{-1}$ (Velimirov *et al.*, 1977). The high productivity and complex biological structure foster an extraordinary diversity of species and interactions within these communities, and there is considerable export of fixed carbon. They support fisheries for a variety of invertebrates and finfish, and the kelps themselves are harvested in many parts of the world.

Kelp genera vary regionally (reviewed by Mann, 1982). Stipitate species of *Laminaria* dominate the North Atlantic, and the coasts of China and Japan. Kelp forests of South Africa, Australia, and New Zealand are dominated by *Ecklonia*, another stipitate genus. Float-

bearing kelps that form surface canopies are important along the west coast of North America, Peru, Chile, and Argentina. The densest surface canopies and largest forests are produced by *Macrocystis*, the dominant genus off Northwest and South America. The Northeast Pacific has the highest kelp species diversity, and its forests often consist of three distinct canopy levels. While rates vary with species (e.g., Mann, 1982; Tegner and Dayton, 1991), all kelps produce considerable amounts of detritus and dissolved organic matter.

Kelp forests are highly dynamic, showing considerable temporal variation, yet resilience to small-scale disturbances results in considerable stability on a time scale of years. Grazing, storms, and El Niño events are important sources of disturbance (Dayton, 1985a). A variety of animals eat kelps, but by far the most important are sea urchins, which are capable of destroying nearly all fleshy algae in most communities (reviewed by Lawrence, 1975; Harrold and Pearse, 1987). Not all urchins have this ability, but most temperate areas have at least one species in this category. Lawrence (1975) found that most instances of severe reduction in plant biomass were associated with increases in echinoid

densities. Potential reasons for increased abundance of urchins included reduced predation, increased recruitment, or immigration of adults in grazing fronts. Disturbances such as major storms or El Niño events affecting the ratio of drift kelp supply to urchin abundance can also trigger the behavioural change to destructive grazing (Ebeling *et al.*, 1985; Harrold and Reed, 1985; Tegner and Dayton, 1987, 1991; Dayton *et al.*, 1992). Whatever the reason, the transition from kelp forest to urchin-dominated “barren grounds” of crustose coralline algae has dramatic impacts on the food and habitat available to the rest of the community. Barren grounds have much lower primary productivity than kelp forests (e.g., Babcock *et al.*, 1999) and may persist for months to years; reforestation begins when urchin populations are affected by alternative foods, strong surge, or disease (Ebeling *et al.*, 1985; Harrold and Reed, 1985).

Thus, factors affecting the abundance of sea urchins and the kelps are critical to the integrity of these ecosystems. Despite the almost universal role of urchins in kelp communities, there is much variation in the types and roles of urchin predators, the existence of urchin competitors, and the effects of human harvest. Many nearshore communities that are accessible from land or with simple boats have been subjected to human fishing for hundreds to thousands of years (e.g., Simenstad *et al.*, 1978; Aronson, 1990; Salls, 1991, 1995; Vadas and Steneck, 1995) and insight into historical changes is critical for understanding contemporary communities. Here we explore potential ecosystem effects of fishing on kelp community structure worldwide, focusing on fishing for urchin predators, urchins and their competitors, and kelp harvest as the taxa with the most direct effects on community structure. We then examine alternative explanations to human impacts on kelp community structure, including variability in climate, recruitment, and urchin disease events. We begin by discussing sea-urchin grazing in different regions, and evidence for the role of predators.

North Pacific

Sea otters (*Enhydra lutris*) are an unequivocal case of significant ecosystem effects caused by exploiting a sea-urchin predator. These mammals, once distributed across the Pacific Rim from northern Japan to central Baja California (Mexico), were hunted to near extinction in the 18th and 19th centuries (Estes and Duggins, 1995). Remnant colonies survived in isolated locations, and after protection in 1911 began to recover. Dramatically different community states on adjacent islands in the Aleutian Archipelago of Alaska with and without sea otters defined these animals as predators capable of causing cascading effects on community structure (Simenstad *et al.*, 1978). In their presence, kelp com-

munities are characterized by a surface layer of *Alaria fistulosa*, a second canopy layer of four species of *Laminaria*, and a prostate canopy usually composed of *Agarum clathratum* (Dayton, 1975). These associations support detritus-based food webs of crustaceans and fish. In the absence of otters, dense populations of sea urchins (*Strongylocentrotus polyacanthus*), along with limpets and chitons, virtually exclude fleshy macroalgae; fish are much less common and usually associated with pelagic food webs. Aboriginal Aleuts arrived in the Aleutian Islands about 2500 years ago, and midden evidence suggests that by about 2000 years ago they had shifted the community from kelp domination to urchin domination by preying on or harrasing the otters (Simenstad *et al.*, 1978).

The role of sea otters in Alaska is clear, because it has been possible to compare situations with and without otters, as well as to observe the transitions that occurred as these mammals expanded their range. After nearly a century of recovery from hunting, sea-otter populations in the Aleutian Islands have declined by 90% since 1990. Estes *et al.* (1998) attribute the decline to increased mortality caused by killer whale (*Orcinus orca*) predation, apparently due to a shift in food availability. Whether this shift is due to fishing, climate change, or a combination, the decline in otters led to the reverse cascade from kelp forest communities to the alternative state of urchin domination.

As clear as the role of sea otters in Alaska kelp forests appears to be, until recently that role was almost certainly modified by interactions with Steller's sea cow (*Hydrodamalis gigas*). Fossils of this species are known from central California to Japan, and their disappearance from most of their range has been attributed to overkill by aboriginal people. These huge sirenians foraged on the kelp surface canopy around the Commander Islands, where they were common until shortly after G. W. Steller first observed them in 1741. Their role in kelp community structure must have been substantial (Dayton, 1975; Simenstad *et al.*, 1978; Anderson, 1995).

Estes and Duggins (1995) examined the generality of the sea otter paradigm by comparing temporal and spatial variability in the Aleutian Islands and southeast Alaska. Despite regional variation in species composition and the abundance of kelps and urchins that affect the trajectories of change between kelp-dominated and urchin-dominated domains, they found the role of sea-otter predation to be predictable and general in its influence on community structure in Alaska. Estes (1996) reports that the pattern is broadly similar for Vancouver Island (Canada) as well. The situation is more complicated in California and Baja California, however. There are episodes of destructive sea-urchin grazing and otters predictably decimate urchin populations here as well, but giant kelp (*Macrocystis pyrifera*) forests also show considerable persistence in the absence

of otters. Foster and Schiel (1988) reviewed 220 surveys outside the otter range in California, and found urchin-dominated or deforested habitats to be the exception (<10% of the sites). They found a range of community states between the extremes identified in Alaska, and the extremes were uncommon. Storms, interannual variability in ocean climate, other physical factors affecting recruitment and growth of kelp, as well as other sea-urchin predators, and echinoid recruitment events and diseases are also important to community structure in California (e.g., Dayton, 1985a; Ebeling *et al.*, 1985; Harrold and Reed, 1985; Tegner and Dayton, 1987).

Native Californians foraged extensively on kelp forest resources and evidence suggests that they also had substantial effects on community structure. Abalones (*Haliotis* spp.) are favoured by both humans and sea otters, and red (*H. rufescens*) abalone shells from middens on Santa Rosa Island in Southern California have been dated at 5370 and 7400 years old (Cox, 1962). Middens contained many sea-otter bones as well as large sea urchins and abalones, prey that would not have been available in the presence of sea otters at their carrying capacity (Salls, 1991, 1995). Native American impact on the Channel Islands was virtually eliminated by Spanish colonization and sea otters were hunted out of Southern California by the middle of the 19th century, leading to the release of sea urchins and abalones from predation. A large (>1800 t in 1879 alone) inter-tidal and shallow sub-tidal abalone fishery began in the 1850s (Cox, 1962).

Sea urchins were not fished until the early 1970s. Although we have no early records of their populations, they probably increased in abundance with abalones after the extirpation of sea otters in Southern California. We do know that *Macrocystis* forests in this region covered extensive areas in the mid-1800s and early 1900s, were relatively stable until the 1940s, and underwent serious declines in the 1950s (Tegner and Dayton, 1991; see maps in Tegner *et al.*, 1996). Systematic diving investigations began in the 1950s, and the proximal reason for the decline was reported to be intense sea-urchin grazing (e.g., North and Pearse, 1970). Two warm-temperate predators, spiny lobsters (*Panulirus interruptus*) and a labrid fish, the sheephead (*Semicossyphus pulcher*), are near the northern boundary of their ranges in Southern California. Gut content studies, laboratory experiments, field observations of urchin behaviour and size-frequency distribution in areas with and without predators, and a sheephead removal study (Tegner and Dayton, 1981; Cowen, 1983; Tegner and Levin, 1983) offer strong evidence for an important role for these predators in the control of sea-urchin populations. Intense fishing has affected the abundance and size distribution of spiny lobsters and sheephead on time scales consistent with the increase in urchin grazing in the 1940s–1950s. This provides a more reasonable explanation than the local extinction of sea otters in the early

19th century (Tegner and Levin, 1983; Dayton *et al.*, 1998). Salls (1991, 1995), excavating through almost 10 000 years of a midden on San Clemente Island, the southernmost Channel Island, found that the early inhabitants extensively exploited sheephead. In one level the size of sheephead bones decreased as their numbers increased; the overlying layer was composed solely of purple sea-urchin (*S. purpuratus*) remains. Salls argues that prehistoric exploitation of this territorial reef fish led to a sea-urchin barren 1050 years ago, but he cannot exclude climatic effects that may have acted in conjunction with fishing.

Sheephead are targeted by spear fishermen, and until recently the primary impact of fishing was on large males (Dayton *et al.*, 1998). In 1988, a market was developed for live fish, which focuses on animals the size of a single entrée; because of their size, female sheephead (many of which may be immature) are heavily exploited. This fishery has grown exponentially, is essentially unregulated, and has the potential for virtual elimination of the sheephead community role. The red sea-urchin (*S. franciscanus*) fishery has greatly reduced destructive grazing episodes of this species (Tegner and Dayton, 1991), but the pressure on sheephead populations suggests that grazing outbreaks by minimally harvested purple urchins may become more frequent.

Northwest Atlantic

The green sea urchin (*S. droebachiensis*) plays a defining role off eastern Canada and New England where alternate community states depend on its population density (reviewed by Elnor and Vadas, 1990; Vadas and Elnor, 1992). When urchins are rare, communities of kelp (*Laminaria* spp.) and other fleshy algae flourish; intensive grazing maintains barrens of mostly encrusting coralline algae. In the early 1970s, a population explosion of green urchins in Nova Scotia and subsequent formation of many coralline barrens co-occurred with a dramatic decline in commercial landings of American lobsters (*Homarus americanus*). This led to the postulate that lobsters controlled urchin populations, that release from this control by overfishing of lobsters led to the destructive grazing, and to considerable research. While much was learned about physical and biological factors affecting kelp–urchin interactions, the lobster model did not survive scrutiny. Predation by one or more species, especially fish, was posed as an alternative hypothesis for the control of green urchins (Elnor and Vadas, 1990).

Historical records show that fishing in the Northwest Atlantic originated onshore and then expanded offshore (Aronson, 1990; Steneck, 1997). Offshore shallow-water refuges from trawling have offered insight into changes in nearshore community structure. Witman and Sebens (1992) compared predation on tethered brittle stars and crabs at coastal and offshore (100 km) rocky ledges in

the Gulf of Maine. Large predatory fish, primarily cod (*Gadus morhua*), but also wolffish (*Anarhichas lupus*), were significantly more abundant at offshore locations, and time-lapse studies indicated that these fish preyed heavily on the tethered invertebrates. Vadas and Steneck (1995) conducted further observations and tethering experiments with different species over a similar range of sites in the Gulf of Maine. Offshore sites had dense stands of kelps and foliose algae, but no large sea urchins, crabs, or lobsters; these invertebrates were orders of magnitude more abundant at inshore sites, where rates of grazing on kelp were also much greater. There was an inverse relationship between sea urchins and both kelp and large predatory fish, and tethering experiments showed higher predation rates on both urchins and lobsters at offshore sites. Big cod and pollock (*Pollachius virens*) were both largest and most abundant at offshore sites; these fish "visited" offshore video recorders more often than intermediate locations and were absent at inshore locations. Wolffish preyed on the largest urchins tethered offshore, and both cod and wolffish preyed on the largest lobsters tested offshore. Inshore prey were all much smaller. To the extent that these offshore "historical relics" reflect past community structure of the nearshore zone, urchin abundance appears to reflect the effects of overharvest of large fish. Keats *et al.* (1986) reported green urchins to be a major dietary component for wolffish in Newfoundland as well.

Witman and Sebens (1992), Vadas and Steneck (1995), and Steneck (1997) review archaeological evidence dating as far back as 4500 years, and historical information, which suggests that coastal predatory fishes (especially cod) were both larger and more abundant in recent historical times than today. The widespread outbreak of sea-urchin populations in the last 30 years in this region is roughly correlated with declines in fish size and stocks. Wolffish were the primary predators of urchins in the experiments, but large cod, pollock, and American plaice (*Hippoglossoides platessoides*) also preyed on them. This suggests that community structure of the Northwest Atlantic was controlled by a suite of large predatory fish species. This hypothesis is not directly testable, but is strongly supported by historical, circumstantial, observational, and indirect experimental evidence. The data do not rule out recruitment variability as a factor in the observed urchin population explosions, but this seems less likely given historical abundance of predatory fish. The marked differences between communities dominated by large predatory fish and kelps versus small predatory fish, crustaceans, urchins, and coralline algae suggest that human exploitation has had wide-ranging ecosystem effects in the kelp communities of the Northwest Atlantic (Witman and Sebens, 1992; Vadas and Steneck, 1995; Steneck, 1997).

Australasia

With no apparent sea-otter analogue in the Southern Hemisphere, it has been suggested that its kelp forests are structured by much simpler two-tiered trophic interactions, with insufficient predation on sea urchins to control their populations (Estes and Steinberg, 1988; Andrew and MacDiarmid, 1991; Steinberg *et al.*, 1995). Algal abundance in two-tiered systems is thus more likely to be under bottom-up control with algae and herbivores having strong selective influence on each other. Steinberg *et al.* (1995) proposed that relative to the North Pacific, the intensity of herbivory should be greater in temperate Australasia, resulting in stronger selection for seaweeds to produce chemical defences, and in turn that Australasian herbivores be more tolerant to algal defences. They indeed found that grazing rates were higher, that kelps and rockweeds (order Fucales) had levels of secondary metabolites about five times greater, and that sea urchins and gastropods were considerably less deterred by phlorotannins in their food than in the North Pacific. Thus, Steinberg *et al.* (1995) conclude that North Pacific and Australasian kelp ecosystems have evolved on fundamentally different tracks, driven by the presence or the absence of intense sea-otter predation on sea urchins.

Jones and Andrew (1990) review the roles of two echinoids that maintain large areas of reef free of large brown algae, *Centrostephanus rodgersii* in New South Wales, Australia, and *Evechinus chloroticus* in northern New Zealand. In both cases, intense non-selective grazing can maintain barrens patches for years, and *Evechinus* removal experiments led to the establishment of *Ecklonia radiata* stands (Andrew, 1988). But the grazing impact of sea urchins in the rest of temperate Australia and of *Evechinus* in southern New Zealand is usually insufficient to create barrens, as these denuded habitats are not common (Jones and Andrew, 1990).

Both spiny lobsters (*Jasus edwardsii*) and demersal fish (primarily the sparid snapper *Pagrus auratus*) prey on *Evechinus* in northern New Zealand (Andrew, 1988; Andrew and MacDiarmid, 1991). From gut content studies, laboratory feeding experiments, and observations of co-occurrence, Andrew and collaborators concluded that the available evidence was insufficient to conclude that predation was regulating urchin populations and thus the frequency of barrens habitat, or that changes in predator abundance would lead to local changes in urchin abundance. Like others, Andrew and MacDiarmid (1991) found the logistics of long-term caging experiments to be infeasible in the nearshore zone.

Nevertheless spiny lobsters and snappers are subject to intense fishing pressure in northern New Zealand (Babcock *et al.*, 1999). These authors recently evaluated community changes in two kelp forest reserves

established in 1975 and 1982. Both predators were significantly more abundant and also larger inside the reserves compared with nearby unprotected areas, and kelp forests occupied a greater proportion of the available habitat. Urchin-dominated areas occupied 14% of the reef substratum in reserves versus 40% in unprotected areas, and for the reserve with previous data, urchin numbers had decreased from 4.9 to 1.4 m⁻² since 1978 in areas formerly dominated by these echinoids. The order of magnitude decrease in barrens habitat between 1976 and 1996 was associated with a 58% increase in primary productivity. Given the importance of kelp to both direct and detrital food webs (Mann, 1982), the ramifications of this change could be substantial. These data strongly suggest that urchin barrens are an indirect consequence of fishing of spiny lobsters and snappers in northern New Zealand. Cole and Keuskamp's (1998) observations of higher *Evechinus* mortality inside reserves support the conclusion that predation can play a key regulatory role. These results are not as dramatic as those caused by sea otters in southeast Alaska, but may be analogous to the Aleutian Islands (Estes and Duggins, 1995), where high rates of sea-urchin recruitment appear to reduce the rate and degree of habitat transition from forest to barrens. At any rate, Babcock *et al.* (1999) have demonstrated that fishing has ecological impacts in northern New Zealand kelp forest communities far beyond the target species. The role of lobsters in other parts of this region is not clear.

South America

Kelp forests of South America have many parallels with those elsewhere (Santelices and Ojeda, 1984a, b) regarding potential competitive domination by a surface canopy (*Macrocystis pyrifera*) and sea urchins (*Loxechinus albus*). In contrast with the assertion in Castilla and Moreno (1982), Castilla (1985), and Contreras and Castilla (1987), urchins do overexploit kelps when occurring at densities above 3–4 m⁻² (they may exceed 100 m⁻²). *Macrocystis* exists in ephemeral patches along the Atlantic coast of southern Argentina and in very large forests along the Beagle Channel and Cape Horn Islands as well as Isla de los Estados, where urchin densities are unusually low with a size distribution skewed toward large animals, suggesting that their larvae are carried away from shore by the Westwind Drift (Dayton, 1985b). *Macrocystis* forests occur in the northern regions of the Chilean fjords where there was intense human fishing pressure on *Loxechinus*. The natural distribution of *Macrocystis* extends well north into Peru (Mann, 1982). Since 1973, Chile has opened the fjord coast to a large sea-urchin trawl fishery, and we know of no research on the present condition of kelp/urchin populations in the region.

Dayton (1985b) confirms Castilla's (1985) observation that South America has no predators that control *Loxechinus* populations. The only predators observed were four *Fusitriton magellanicus* consuming small urchins (Castilla, 1985) and *Myenaster gelatinosus*, which does prey on *Loxechinus* but inefficiently because of effective escape behaviour (Dayton *et al.*, 1977). The question is open as to whether predation has ever been effective. Dayton (1985b) mentioned the possibility that the large lithodid crab (*Lithodes antarctica*), which was often observed eating bivalves, asteroids, and urchins, may once have occurred in sufficient density to have affected sea-urchin populations before being virtually eliminated by fishing (Compodónico, 1981). Darwin's (1860) reports of large kelp forests may have been stimulated by what he saw in the south or perhaps there were predators that controlled urchin populations in the fjord region.

Subantarctic islands

Many of the Subantarctic Islands, including the Falklands, Chathams, Gough, Tristan da Cunha, Marion, Kerguelen, Macquarie, and the Auckland Islands, are reported to have large *Macrocystis* forests (reviewed in Dayton, 1985a). The lack of a build-up of sea urchins can be attributed to the strong Westwind Drift that sweeps away long-lived urchin larvae and the absence of appropriate up-current larval source areas.

South Africa

Kelp communities of western South Africa are composed of extensive forests of *Ecklonia maxima* and *Laminaria pallida*. With strong upwelling, a high kelp production to biomass ratio, and an extremely energetic wave environment, most production enters detritus food webs and suspension feeders are the dominant consumers (Velimirov *et al.*, 1977). The small standing crop of grazers indicates that little kelp production is passed on to debris feeders, although sea urchins (*Parechinus angulosus*) are the most abundant benthic grazers. *Parechinus* does not form feeding fronts but does produce isolated barren patches of a few to tens of metres in 8–15 m depths. Because the prevailing swells apparently knock urchins off large plants, their impact is limited to grazing on kelp recruits. Anderson *et al.* (1997) review estimates that *Parechinus* consumes 14–20% of the annual production of *Ecklonia*. The most important predator in the system is the rock lobster (*Jasus lalandii*), whose main diet is mussels; it in turn is preyed on by seals, cormorants, dogfish, and octopus, and is also fished by humans (Velimirov *et al.*, 1977).

Anderson *et al.* (1997) revisited the role of *Parechinus*, suggesting that the energy flow models that dominated earlier research missed important structuring processes,

and that previous focus on the west coast of South Africa was less relevant in the warmer water east of Cape Point. East of Cape Point, benthic grazers (mainly urchins) are more abundant, *Parechinus* are common in shallow water, and juvenile *Ecklonia* are found in disproportionately high abundance on holdfasts of adults relative to available rock surface. There is also an inverse relationship between the cover of understory algae and grazer densities. The immediate implications pertain to kelp harvesting, which leads to holdfast death; kelp recruitment is limited or delayed where benthic grazers are numerous. This indicates a more important role for grazing, primarily by sea urchins, in this region, and suggests that *Parechinus* could prevent recolonization of areas cleared of kelp by harvesting or extreme storm damage (Anderson *et al.*, 1997). The fundamental differences in structuring processes between west and south-east coast kelp forests were underscored by recent increases in *Jasus* abundance, which coincided with the virtual disappearance of *Parechinus* at sites on the south-western Cape (Tarr *et al.*, 1996). Anderson *et al.* (1997), predicting increases in kelp recruitment and understory algal cover, suggest that *Jasus* is capable of causing a trophic cascade in the southwestern Cape region.

Fisheries for abalones and sea urchins

Abalones share similar food and habitat preferences with sea urchins in kelp forests of the North Pacific, Australasia, and South Africa. Abalones, however, feed primarily on drift algae and probably have little effect on attached plants (Lowry and Pearse, 1973). In the North Pacific, abalone and urchin abundances sufficient to support fisheries clearly resulted from elimination of sea otters by prehistoric or modern hunters (Estes, 1996). Fisheries for abalones predate those for urchins in many areas; thus, an obvious question is the effect of abalone fishing on kelp community structure. Salls (1991) found prehistoric evidence for over-exploitation of abalones below younger midden layers dominated by urchin remains. In Southern California, intensive shallow water abalone fishing by non-native Americans took place from 1850 to 1900 (Cox, 1962). Commercial abalone fishing with modern gear began in the 1940s, maintained high annual landings until the late 1960s, and then began a precipitous decline (Dugan and Davis, 1993). The apparent sea-urchin population explosion in the 1950s and 1960s may have partially resulted from reduced competition with abalones (North and Pearse, 1970). Sea urchins clearly have a detrimental effect on other grazers when food is limiting, but when food is abundant, abalones may out-compete sea urchins for space (Lowry and Pearse, 1973). Fishing for red sea urchins began in the early 1970s in Southern California (Tegner and Dayton, 1991), expanded to Northern California in the late 1980s, and has been the largest fishery in the

state for most of the 1990s. The Southern California fishery has greatly reduced the distribution and abundance of red urchins, but potential ecosystem impacts have been obscured by the grazing of non-exploited urchin species, and climatic effects on kelp resources (e.g. Tegner *et al.*, 1996, 1997).

Severe overfishing of abalones has made field studies of competition with sea urchins impossible in Southern California. The north coast (San Francisco to the Oregon border) has been reserved for recreational abalone fishing since 1945. Access restrictions allowing only free-diving and shore-picking established a *de facto* depth refuge (Karpov *et al.*, 1998) that maintained high levels of red abalone sport harvest in this region. Prior to the north coast sea-urchin fishery, red urchins dominated rocky bottoms below 6–7 m. After urchin fishing began, there was substantial algal recruitment to depths of about 20 m, expanding abalone habitat and food supply. Red abalone densities have increased significantly in shallow, high-use areas of the north coast in the 1990s, suggesting release from competition with red urchins (CDFG, 1998).

Concern by fishermen that urchin-dominated barren grounds were increasing in New South Wales at the expense of abalone habitat led Andrew *et al.* (1998) to conduct a *Centrostephanus* removal experiment. Thirty replicates of at least 1000 m² were used to compare different patterns of urchin removals. Clearing the echinoids led to a habitat shift from coralline crusts to a range of foliose algae. Habitat change was accompanied by an order-of-magnitude increase in abalones. Given that barrens habitat occupies up to 50% of nearshore reefs, these results suggest that urchins limit the productivity of the abalone fishery. An incipient sea-urchin fishery offers the potential of enhancing the more valuable abalone fishery, and Andrew *et al.* (1998) advocate development of an experimental approach to co-management of the two species.

The relationship between abalones and sea urchins involves more than competition. Juvenile abalones shelter under the spine canopy of adult urchins in California (Tegner and Dayton, 1981), Japan (Kojima, 1981), and South Africa (Tarr *et al.*, 1996). The importance of this shelter was recently illustrated in South Africa, where the apparent invasion of *Jasus* led to the virtual disappearance of *Parechinus* and simultaneous loss of juvenile (<30 mm) *Haliotis midae* in two of four main abalone fishing grounds. Day (1998) showed experimentally that urchin removal resulted in dramatic local declines of abalone juveniles and recruits. She found that juveniles benefit from the association through protection from predators, an enhanced food supply, and reduction in the amount of time they need to spend exposed while feeding. The Southern California sea-urchin fishery may have contributed to abalone recruitment failure through reduction of juvenile habitat.

Fishing in the Gulf of Maine has shifted from predatory groundfish such as cod to American lobsters (an intermediate predator) and, starting in the late 1980s, to green sea urchins (Steneck, 1997). Whereas the top trophic level is now functionally absent from the coastal zone and lobster landings have remained high or increased, fishing has caused significant declines in urchin abundance, resulting in increases in kelps and other macroalgae. Expanded kelp forests have led to increased productivity and macroalgal detritus, and a shift in lobster sheltering to kelp beds (Steneck, 1997). Thus, the urchin fishery and extended kelp beds may present a significant expansion of lobster habitat in coastal zones. Kelp forests are also nursery grounds for juveniles of some large predatory fish and, recently, pollock were seen for the first time in 20 years at sites formerly devoid of kelps. This suggests that reduced herbivory and increased macroalgal stands may affect recruitment potential and resilience of groundfish stocks (Steneck, 1997).

Kelp harvesting

Macrocystis pyrifera has been harvested since the early part of the 20th century in Southern and Central California and Baja California. The regulated harvest cuts only the upper 1.2 m of the surface canopy. This usually has no measurable impact on the plants or on the benthic community (Dayton *et al.*, 1998). The canopy, however, is an important initial recruitment habitat for several fish species (Carr, 1991); direct impacts of kelp harvesting on these sensitive stages is unknown. Depending on the season, high growth rates lead to rapid (days to weeks) reformation of the canopy. Whether juvenile fish shelter around kelp fronds lower in the water column or face increased vulnerability to predation during the interim is an important unresolved question regarding the ecosystem effects of kelp harvesting.

Kelps are widely harvested, and population impacts are dependent on the frequency, intensity, and percentage removal as well as life-history attributes of the target species (reviewed by Vasquez (1995)). Harvest is similar to physical and biological disturbance in that both affect the dominant population and modify the distribution and abundance of associated plant and animal species. Many ecosystem effects relate to details such as the timing of harvest relative to kelp reproduction, or the presence of benthic grazers. Given the high susceptibility of kelp forests to natural disturbances, well-managed kelp harvest appears relatively benign.

Natural processes affecting community structure

Global kelp distributions mirror those of cold, nutrient-rich waters, and productivity is sensitive to variability in

oceanographic conditions (Tegner *et al.*, 1996). Lower latitude kelp forests of both North and South America are greatly affected by El Niño events (reviewed by Tegner and Dayton, 1987; Dayton and Tegner, 1990). Strong El Niños such as the 1982–1984 event are associated with greatly increased temperatures, depressed thermoclines that render upwelling ineffective, and anomalous levels of poleward flow. Temperature anomalies of up to 11°C caused mass mortality of *Macrocystis integrifolia* and associated animals off the coasts of Peru and northern Chile. Anomalies of 4–5°C led to canopy loss and considerable mortality of *M. pyrifera* off the coasts of Baja California and part of Southern California; temperatures further north remained within the range of suitability. Extraordinary storms during the 1982–1984 and 1997–1998 events further devastated kelp forests along most of the coast. These large-scale, low-frequency events of ocean climate have many effects on the kelps (Tegner *et al.*, 1997) and on component animal populations. Important implications for community structure include greatly enhanced recruitment of spiny lobsters and sheephead in Southern California (Tegner and Dayton, 1987; Dayton and Tegner, 1990).

Factors affecting sea urchins and critical to kelp community structure include strong recruitment, which is often associated with anomalous oceanographic conditions, storm-induced mortality, and disease. Evidence that very large urchin recruitment events can swamp other mechanisms regulating their numbers, thus leading to deforestation, comes from southwestern Canada (Foreman, 1977), Nova Scotia (Hart and Scheibling, 1988), and California (Watanabe and Harrold, 1991). Thus, regional differences in predictability of recruitment may account for some of the variation in occurrences of urchin barrens (Watanabe and Harrold, 1991). Severe storms may cause massive urchin as well as kelp mortality (Ebeling *et al.*, 1985). Mass urchin mortalities have been followed by reforestation in California (Pearse and Hines, 1979; Dayton *et al.*, 1992), and Nova Scotia (e.g., Scheibling, 1984). Indeed, Scheibling (1984) suggests that a sea-urchin pathogen is the critical mechanism for the switch from barrens to kelp forest in the Northwest Atlantic and notes the importance of ocean temperature in triggering epizootics and the extent of mortality. Similarly, increases in alternative food sources, such as diatoms, drift algae from nearby areas, or simply intense kelp recruitment may reduce grazing pressure enough to allow recovery of kelp populations (Harrold and Reed, 1985).

Discussion

Understanding the ecosystem effects of fishing in kelp forest communities presents spatial and temporal

challenges. First, each region discussed encompasses significant biogeographic variation in the physical and biological factors controlling community structure. Examples include regional species differences in urchin predators in the Northeast Pacific, and the important role of temperature in urchin disease outbreaks (Scheibling, 1984), correlating with latitudinal variability in persistence of barrens in the Northwest Atlantic (Keats *et al.*, 1986). Second, as highly accessible habitats, kelp forests have been fished with intensities sufficient to alter community structure for hundreds of years. Reliance on properly controlled manipulative field experiments in existing ecosystems without pristine controls will almost certainly fail to elucidate the natural structuring mechanisms as they evolved, yet understanding of what natural resources could or should be underlies all management actions. Unless we use all available information to reconstruct pre-harvest states, the expectations based on a reduced resource will be inappropriate reference points for evaluating overfishing or other disturbances, as well as establishing objectives for restoration (Dayton *et al.*, 1998).

Sea otters are an uncontested example of human harvest of a single species having dramatic ecosystem impacts. In other cases, there is strong evidence that exploitation of multiple predators (spiny lobsters and snappers in northern New Zealand and several demersal fishes in the Gulf of Maine) led to release of urchin populations and trophic cascades. It is likely that fisheries for both predators and competitors affected urchin populations in Southern California. Field experiments of the appropriate scale to show ecosystem effects have been difficult in most cases and suffer from fishery interactions. The top trophic level is functionally absent from vast reaches of the Gulf of Maine (Steneck, 1997). In other cases, urchin predators are still present, but at greatly reduced abundance with a shift to smaller sizes, their community roles are different and they may be unable to convert an urchin barren to a forested habitat (e.g., Tegner and Levin, 1983; Dayton *et al.*, 1998; Babcock *et al.*, 1999). Similarly, abalones have been overfished almost worldwide, but two areas where they have been better managed (New South Wales and Northern California) support midden evidence for a role for competitors in curbing sea-urchin populations (Andrew *et al.*, 1998; CDFG, 1998).

That disease has controlled urchin populations in Nova Scotia and elsewhere in recent years is unequivocal, but this reality does not eliminate ecosystem effects of fishing. Plagues are generally thought to be catalysed by overcrowding (e.g., McNeill, 1976); in nature this is often a result of reduced predation. Northwest Atlantic cod, especially coastal populations, were heavily fished by Europeans as early as the 16th century, and cod and associated species have been overexploited throughout the region (Kurlansky, 1997). The onshore-offshore

differences in large fish and community structure observed in the Gulf of Maine (Witman and Sebens, 1992; Vadas and Steneck, 1995) have not been reported for Nova Scotia (Elnor and Vadas, 1990). Whether this represents biogeographical differences, the absence of offshore refuges, or a lack of investigations into the role of cod and associates is not known. It is important not to generalize along biogeographical gradients, but it is equally important to ask the right questions. As with disease, it is unequivocal that oceanographic variability on scales ranging from storms (e.g., Ebeling *et al.*, 1985) to El Niño events affects kelp availability (e.g., Tegner *et al.*, 1996), and thus the ratio between food and grazing pressure (e.g., Harrold and Reed, 1985). Strong urchin recruitment events (e.g., Watanbe and Harrold, 1991) can also trigger the shift between kelp forest and barrens.

In many cases, we may never understand the entire range of effects of fishing on the kelp ecosystem because important species (such as Steller's sea cow) are extinct (Anderson, 1995), or so severely depleted (e.g., giant sea bass [*Stereolepis gigas*] off the coast of California [Dayton *et al.*, 1998]) that we can only guess at their community roles. Determination of the role of sea otters was delayed for at least a century because they were hunted to near extinction, but as they recovered understanding was facilitated by their discontinuous distributions and changes that have taken place in recent decades. California kelp forest communities are missing many animal species, including most of the large fishes and several large invertebrates that once were common (Dayton *et al.*, 1998). Whether or not they had direct impacts on the kelps, they may have had diverse types of indirect impacts on the community that no longer can be studied. There is a challenge to biologists to identify these ghosts and their lost biological interactions.

Overfished coastal habitats with altered community structure are not restricted to kelp forests, and no-take marine protected areas have been critical for determining natural community-structuring interactions in other habitats where sea-urchin grazing has caused trophic cascades. These include macroalgal areas of the Mediterranean (Sala *et al.*, 1998) and Kenyan coral reefs (McClanahan and Shafir, 1990). Areas with and without predators have been critical to the understanding of predator roles in kelp forests in Alaska (e.g., Simenstad *et al.*, 1978), New Zealand (Babcock *et al.*, 1999), and the Gulf of Maine (Witman and Sebens, 1992; Vadas and Steneck, 1995; Steneck, 1997). The north coast region of California, which is a *de facto* abalone reserve (CDFG, 1998), offers information about the role of sea-urchin competitors. Protected areas offer a benchmark with which to separate anthropogenic from environmental change, as well as mechanisms for testing different management tools. They also offer an opportunity to improve management designed to protect

community structure and function. And without fishing restrictions in areas of sufficient size to allow recovery of functionally extinct species, their biology and ecosystem roles will never be known.

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