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SLIDING BASELINES, GHOSTS, AND REDUCED EXPECTATIONS IN KELP FOREST COMMUNITIES

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Abstract. The detection of trends in ecosystems depends upon (1) a good description of the foundation or benchmark against which changes are measured and (2) a distinction between natural and anthropogenic changes. Patterns and mechanisms observed over 25 years in a large kelp forest suggest that definition of a meaningful benchmark is impossible, because many of the large animals have been gone for years to decades, and kelps are sensitive to large-scale, low-frequency El Niño–Southern Oscillation events and longer term regime shifts. A shift in the oceanographic climate has significantly reduced the average size and carrying capacity of the dominant plant. The animals that have been functionally removed from the community include sea otters, black sea bass, yellowtail, white sea bass, and abalones. Other species are still present, but fisheries have had huge effects on the abundances, size–frequencies, and/or spatial distributions of sheephead, kelp bass, rays, flatfish, rock fish, spiny lobsters, and red sea urchins. Now even sea cucumbers, crabs, and small snails are subject to unregulated fishing. The plants continue to exist without a hint of the effects of the loss of so much animal biomass. Furthermore, most of the megafauna have been removed with very little documentation or historical understanding of what the natural community was like. Thus, our ability to separate anthropogenic impacts from the “natural” dynamics of the system is severely compromised. We discuss the importance of both an ecosystem focus on productivity and careful monitoring of as many populations as possible. In addition, we show that this community is not tightly integrated with mutual dependencies; hence, many species can be removed without much affecting the rest of the ecosystem.

Key words: *baseline; benchmark; biodiversity; climate; elasmobranchs; fish; fishing; kelp; regime shift; trends.*

INTRODUCTION

Any measure of change in a natural ecosystem must be grounded upon a well-defined natural standard or benchmark against which potential changes are measured and evaluated in relation to natural variation in the system. This is difficult because ecosystems are composed of many populations, each of which is affected by changes in the physical and biotic components of the environment. How does one define a natural benchmark against which change must be evaluated? How does one discern natural from anthropogenic disturbances and changes? This is particularly vexing in marine systems, which are especially sensitive to nutrient availability and productivity, and in which natural variation is often extreme. Furthermore, logistic restraints severely restrict benchmark studies, such that the long-term data necessary for a meaningful measure of the natural state are usually lacking. This paper describes a well-known marine system for which any

measure of a benchmark is represented by a moving target of reduced expectations of what really is the natural standard. In addition, rare, episodic events have important consequences that result in a highly variable baseline amidst much background noise.

The Point Loma kelp forest off San Diego, California, USA, represents an interesting coastal example because it is unusually well studied over a relatively long time period (Tegner et al. 1996a). Here, we discuss trends in the population of *Macrocystis pyrifera*, the competitive dominant kelp species contributing most of the structure and productivity to the community. We summarize long-term population data suggesting that changes in the oceanographic climate have resulted in significant changes in *Macrocystis* carrying capacity. In addition to important natural changes, we discuss massive anthropogenic impacts that have virtually eliminated most of the large faunal components of the natural system.

Like most communities, kelp forests are structured by physical and biological processes. The distribution of kelps is constrained by physical factors including light, substrata, sedimentation, nutrients, water motion,

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salinity, and temperature. These physical factors have interdependent thresholds that are both important and difficult to study. The cascading relationship between sea otters, kelps, and sea urchins is the best known biotic structuring agent (McLean 1962). In this example, sea urchins potentially eliminate kelp populations from particular habitats, in the absence of otter predation on urchins. The alternate states of this community, kelps or urchin barrens, can persist for a long time in Alaska (Simenstad et al. 1978). This simple dichotomy of stable, alternate states is not as clear in southern California, where only a small fraction of the area without sea otters is deforested by sea urchins (Foster and Schiel 1988, Foster 1990), and other predators have apparently controlled sea urchin populations (Tegner and Dayton 1981, Cowen 1983, Tegner and Levin 1983). Now there is evidence that the competitively dominant *Macrocystis* is sensitive to changes in oceanographic climate (Tegner et al. 1996a, 1997), and the detection of trends relies on understanding oceanographic climate as well as the availability of meaningful benchmark standards. This paper discusses the implications of oceanographic climate and the long history of human intervention, which cannot be well quantified, but has resulted in the virtual elimination of many of the animal components of the community. Thus, we are left with an assemblage of plants, ghosts of the megafauna, and no quantitative understanding or benchmark standards for how the natural community should function. We argue that this may be true for many coastal marine communities.

LONG-TERM PATTERNS OF DENSITY AND DISTRIBUTION

Evidence for long-term changes in coastal ecosystems must be evaluated in relation to sometimes massive disturbances from storms, El Niño–Southern Oscillation (ENSO) events, and long-term regime shifts within the overlying oceanographic climate, as well as the many types of anthropogenic impacts. The Point Loma kelp forest is heavily harvested for alginates, sometimes exposed to pollution, and subjected to intense recreational and commercial fishing for almost all species of larger animals.

The giant kelp, *Macrocystis pyrifera*, grows long stipes and forms dense, floating canopies in many temperate parts of the world. The stipes and canopy not only form habitats for many other species, but also affect currents and waves in the surrounding ocean. This creates important edge effects that influence flow patterns and transport of nutrients and larvae. These edge effects, as well as gradients in depth and covarying physical parameters, may result in regional differences in community structure. In addition to the dominant *Macrocystis*, the system includes distinct patches of understory kelps that can be large, surprisingly abundant and resilient, and also variable with depth (Dayton et al. 1984, 1992).

Over the last century, the Point Loma kelp canopy has undergone frequent fluctuations, ranging from being essentially absent at least three times to covering almost 10 km² (North et al. 1993, Tegner et al. 1996a). We have also documented such temporal fluctuations in population densities of *Macrocystis* and the understory kelps *Pterygophora californica* and *Laminaria farlowii* (Fig. 1a–d). Although it is not apparent in such density data, kelps often recruit in cohorts that have important consequences on succession and mortality patterns that might last for years. The large amount of variability is obvious, yet these populations represent the major structuring components of the system.

MECHANISMS DETERMINING PATTERNS

Physical factors

Abiotic factors exert important effects on (1) germination and survival of very small sporophytes, (2) growth and fecundity, and (3) survivorship of adult plants. Relevant physical parameters include light, nutrients, temperature, and physical damage from sediment scour and storms. These parameters have been evaluated in different cross-shore and long-shore regions of the kelp forest. Long-shore differences are an issue because the more variable southern part of the kelp forest is apparently more stressed than other regions, probably by its proximity to the mouth of San Diego Bay, a large naval and commercial port (Dayton et al. 1992). In each case, depth and region might be expected to correlate with important differences in these parameters. In general, the major sources of interannual variability in kelp populations are water temperature, severe storms, and El Niño events that may include storms and 1–3 years of warm, nutrient-depleted water.

Light.—San Diego's outfall monitoring program collects Secchi disk data along the outer edge of the kelp forest. There was no correlation between light penetration and mass emissions from any of the regional sewage outfalls from 1973 to 1987 (Conversi and McGowan 1994), or with the kelp harvest at Point Loma from 1977 to 1994 (Tegner et al. 1996a). Our unpublished measurements of integrated benthic quantum irradiance show important interference with light transmission by the canopy, as well as reduced transmission in the southern part of the kelp forest near the mouth of San Diego Bay.

Temperature and nutrients.—Temperature is inversely related to the concentration of nitrate, the nutrient that limits kelp growth. Nitrate is not detectable above 16°C in this region, and the inverse relationship in published temperature–nitrate plots allows the use of temperature as a surrogate for nitrate–nitrogen availability (see Tegner et al. 1996a, 1997). In situ records reflect the significant increase in temperature with the 1982–1984 ENSO and decreasing depth, and the seasonal cycle of coldest bottom water during the spring/

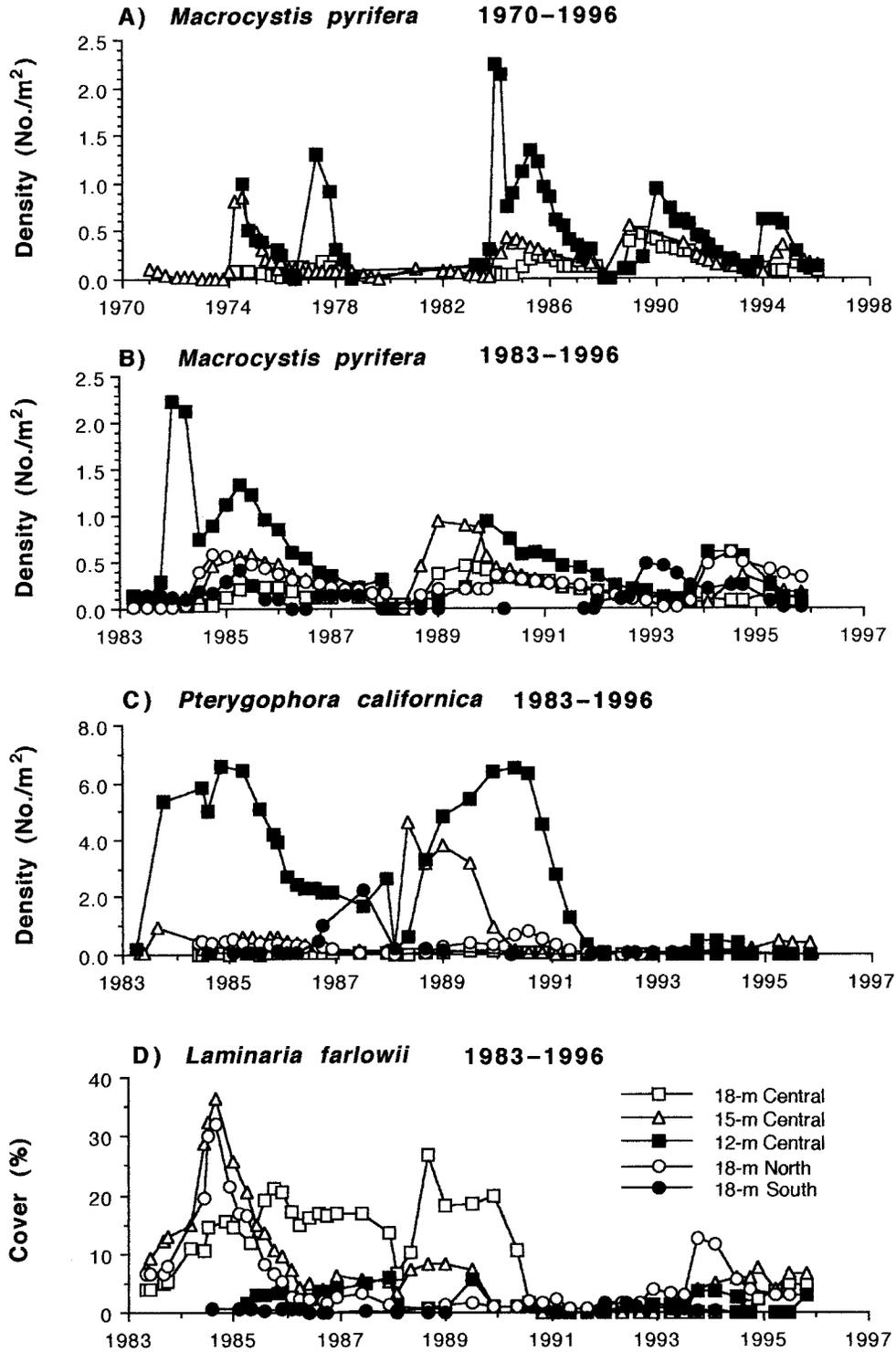


FIG. 1. (A) Time series of *Macrocystis pyrifera* densities at three depths in the center of the Point Loma, California, kelp forest, 1970-1995. These data are from individual transects and have no variance. (B-D) Density means for three kelp species from four large transects at each of five sites (the same central sites plus sites at either end of the forest), 1983-1995, have fairly tight error bars (see Tegner et al. 1997).

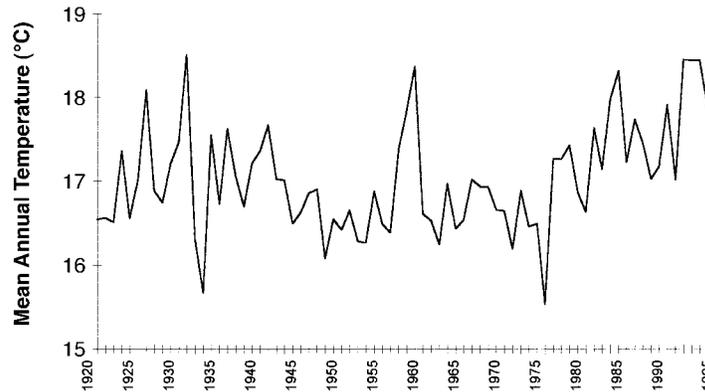


FIG. 2. Annual means of surface temperature from the Scripps Institution of Oceanography pier, 1920–1995. Although there is considerable interannual variability, average temperature has clearly been rising since the onset of the regime shift in about 1976 (McCall 1996).

early summer, followed by a rise in the late-summer/fall and isothermal conditions during winter. Note that sea surface temperatures were especially warm during 1983–1985 and 1992–1994, and relatively cool during 1988–1989 (Fig. 2). Relatively small differences in average temperatures have major implications for *Macrocystis* productivity (Tegner et al. 1996a, 1997).

ENSOs.—El Niños are low-frequency, large-scale events that have proven difficult for oceanographers to predict; they originate in the tropics, but have global consequences (Glynn 1990). The 1982–1984 ENSO was the largest in at least a century and included a series of dramatic storms. Storm-caused mortality of *Macrocystis* (Dayton and Tegner 1984a, Seymour et al. 1989; Table 1) showed consistent depth-related patterns, with the highest mortality (66%) in shallow water, 47% mortality in central 15-m depths, and the lowest mortality (13%) at the 18-m site. These mortalities were also age specific, with the highest mortalities occurring in the young and older plants (Dayton and Tegner 1984a).

Warm, nutrient-poor water is the most characteristic component of El Niños, and it had devastating effects on the Point Loma kelp forest in 1983–1984. Bottom temperatures were $>16^{\circ}\text{C}$ for several months, whereas surface temperatures approached the middle of the 20–30°C range. *Macrocystis* fronds deteriorated, first in the canopy and then throughout the water column, until

plants that survived the storms, as well as new recruits, suffered high mortality (Tegner and Dayton 1987). This mortality also was region specific: the long-shore edges of the kelp forest had lower mortality, probably reflecting slightly greater nutrient availability (Jackson 1977), whereas the central part of the forest had higher mortality.

Storms.—A short but very intense storm in January 1988 was the most severe storm in ~200 years; the *Macrocystis* mortality was much greater than that for all of the winter 1983 ENSO storms combined, and this was the first large-scale storm-induced mortality of the understory in several decades. By decreasing the supply of drift algae, the storm resulted in intense grazing by sea urchins on live kelps (Tegner and Dayton 1991, Dayton et al. 1992). Again, there were strong depth and regional patterns of survivorship (Table 1, Fig. 1). However, this storm was a new type of disturbance within our time frame; at the 8- and 12-m sites, surge and sand scour eliminated an extraordinarily high proportion of plants, and in many cases as much as 1 cm of the substratum was blasted away (Dayton et al. 1989). Patches of kelps, some marked in 1971, were obliterated, and heavy kelp recruitment appeared to restart the entire community. This also happened on most of the baseline transects at 15 m, yet all of the old patch boundaries at 15 m that were tagged in 1971–1972 and for which the markers survived, eventually recovered

TABLE 1. Percentage winter mortality of adult *Macrocystis pyrifera*, with *N* values in parentheses. Age-specific mortality rates are not included. A dash indicates that no kelps were present, because of sea urchin barrens (see *Introduction*). Giant kelp suffers a surprising amount of mortality; there are patterns and differences in time and region of the kelp forest, especially in the southern region, which was often overgrazed by sea urchins.

Site	1982–1983	Nov–Mar 1983–1984	Nov–May 1984–1985	Dec–Apr 1985–1986	Dec–Jun 1986–1987	Dec–Feb 1987–1988	Sep–Jun 1988–1989	Nov–May 1989–1990
18-m Central	13 (52)	15 (20)	25 (16)	40 (89)	4 (49)	65 (42)	0	23 (172)
15-m Central	47 (40)	27 (51)	23 (167)	31 (188)	13 (90)	69 (72)	0	26 (228)
12-m Central	66 (80)	66 (446)	8 (171)	37 (169)	29 (71)	94 (41)	0	23 (186)
18-m North	40 (14)	50 (12)	20 (217)	23 (175)	11 (90)	89 (67)	8 (56)	11 (83)
18-m South	41 (100)	35 (42)	77 (166)	—	55 (31)	87 (31)	—	—

and persisted with similar configurations. The mechanisms are not clear, but the resilience of these patches at 15 m is remarkable. Storm disturbance at 18 m was less intense; although no patches had been delineated earlier, most seemed to persist (Dayton et al. 1992).

Oceanographic climate

Substantial changes in oceanographic climate occurred throughout the Holocene (Pisias 1978), suggesting that most of the populations in this ecosystem are adapted to considerable environmental stress. In addition to recognizing these and shorter term sources of variation, it is important to distinguish anthropogenic impacts from natural trends. If long-term trends are related to changes in seawater temperature and its covariate, nutrient availability, we might be able to tease apart natural background changes from those due to anthropogenic change. Annual average surface temperature (Fig. 2) was significantly correlated with kelp harvest, but it explained only 24% of the variance, suggesting that other variables were in play (Tegner et al. 1996a). Because the canopy is very vulnerable to disturbances that may not affect plant survivorship, we considered two subsurface measures of kelp "well being:" (1) stipe number as an index of individual plant growth, and (2) stipe density as a measure of the carrying capacity of the system at any time and place. Both stipe measures were sensitive to interannual variability in surface temperature (nutrients) between 1983 and 1995, and were much more sensitive than plant survivorship (Tegner et al. 1996a).

Two massive disturbances afforded us the opportunity to measure the consequences of oceanographic climate events on patterns of succession and growth. Both the 1982–1983 ENSO storms and the 1988 storm caused massive mortalities of all species of kelps at Point Loma. Each disturbance was followed by intense recruitment that resulted in easily identifiable cohorts; each of these cohorts was established in different oceanographic regimes. Warm El Niño years in 1982–1984 were followed by a "normal" oceanographic period. However, the 1988–1989 period following the destructive storm was a cool, nutrient-rich period termed a "La Niña." Finally, a modest 1992–1993 El Niño period was followed by an anomalously warm 1994 (Fig. 2).

Comparison of the cohorts following the El Niño and

the 1988 storms showed that stipe carrying capacity was much higher during the La Niña conditions of 1988–1989 than during the "normal" 1985–1986 conditions, but that the 1988 cohort, instead of leveling off at the higher level, declined through the warm years of 1991–1994 and then recovered somewhat in 1995 (Tegner et al. 1996a, 1997). The log of plant size (number of stipes per plant) vs cumulative percentage for four size–frequency distributions (Fig. 3) shows that the median size has decreased by about two-thirds since 1957. There is a strong inverse relationship between plant size and density, so it is important to compare plant densities among these years. Despite the differences in size, the large 1957 plants were actually growing at the same density as the smaller 1993 plants! We found a strong inverse relationship between median stipe number and surface temperature anomalies, calculated quarterly and summed over three years for the populations sampled since 1957. This strongly suggests very different carrying capacities for kelp (Tegner et al. 1996a, 1997). It is clear that there are large differences in oceanographic climate between the 1950s and the 1990s (Roemmich and McGowan 1995). John Isaacs used the term "regime" to describe distinct environmental or climatic states, and regime shift has come into acceptance for describing abrupt transitions between regimes (McCall 1996, Steele 1996). Our kelp data are consistent with the regime or climate shift (Hayward 1997) that began in the mid-1970s.

Biological factors

Patch dynamics and lag effects in succession.—Understorey algal populations are affected by the *Macrocystis* canopy, which exerts strong dominance in competition for light under moderate levels of wave exposure. This is certainly true on the scale of the 8–10 × 1 km *Macrocystis* forest at Point Loma. However, on a smaller scale, patches of understorey kelps may exclude recruitment of *Macrocystis*; the shallow and deeper limits of giant kelp may be constrained by such competition as well as physical limitations. The exclusion has been demonstrated to result from both competition for light and limits to natural dispersal of spores; kelp recruitment is also inhibited by thick coralline turf (Dayton et al. 1984). Localized differences in habitat can result in variability in recruitment, succession, and survivorship. One interesting source of spatial and temporal variability following large disturbances is the predictable outbreak of an ephemeral brown alga, *Desmarestia ligulata*, which can delay successional processes for time lags of up to a year. Other patches are composed of much longer lived plants, and their inhibition of succession can last for decades (Dayton et al. 1992). These lag effects, however, are susceptible to considerable modification by the oceanographic climate during succession (Tegner et al. 1996a, 1997).

TABLE 1. Extended.

Nov–May 1990–1991	Sep–May 1991–1992	Nov–Mar 1992–1993	Sep–Jun 1993–1994	Aug–Mar 1994–1995
22 (116)	15 (82)	4 (52)	24 (45)	74 (34)
32 (120)	28 (82)	20 (49)	33 (32)	14 (139)
29 (101)	37 (70)	32 (31)	55 (11)	50 (103)
10 (118)	43 (95)	66 (32)	100 (3)	17 (171)
—	—	15 (240)	18 (123)	67 (95)

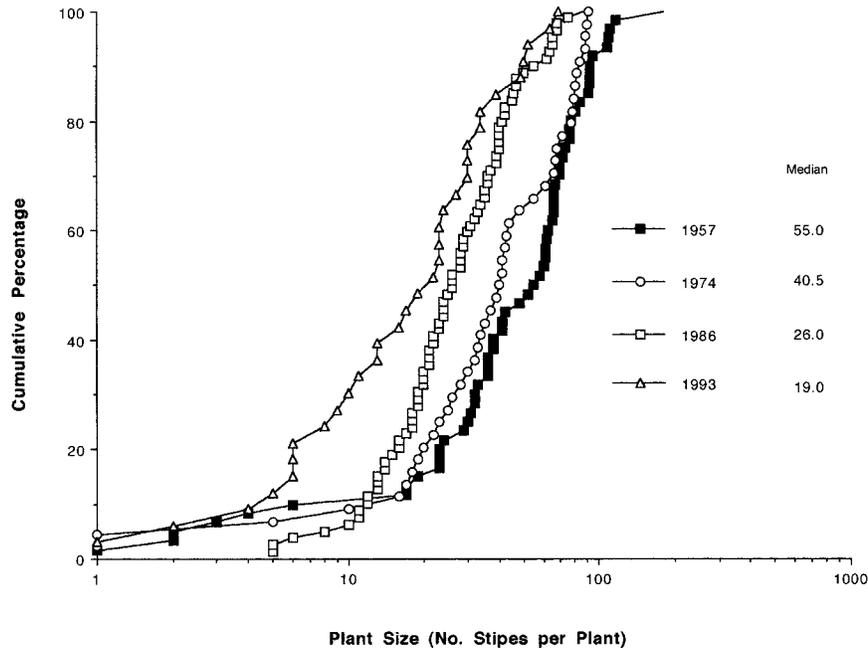


FIG. 3. Cumulative percentage for size–frequency distributions collected in four different years vs. *Macrocyctis pyrifera* size, on log scale (see Tegner et al. 1996a). The key indicates median size per sample year.

Sea urchin grazing.—Kelp populations appear to be unique among plant communities because they are vulnerable to being destroyed by a single type of herbivore: sea urchins. Areas ranging from hectares to kilometers to entire coastlines are denuded of macroalgae by these grazers. These barren areas, which may persist for many years until the urchin population is reduced by predation, disease, or storms (Simenstad et al. 1978, Ebeling et al. 1985, Schiebling 1986), are well known in all the world's kelp habitats (Dayton 1985a). In most natural situations, sea urchins do not exert this effect because they remain in crevices and under rocks offering protection from predators; indeed, sea urchins and their predators at Point Loma have usually achieved a balance allowing kelp persistence. The historical predators were sea otters, spiny lobsters, and sheephead fish; otters are completely absent today and populations of the other two predators are so altered by fishing that their ecological roles are much reduced. If urchins in protected habitats obtain adequate drift algae, they do not emerge to forage. Because urchin larvae are planktonic for over a month, they are additional sources of variation. Finally, recruitment varies are typical of lobsters and sheephead, the important extant predators of urchins, which in some parts of southern California recruit only when large El Niños push southern water masses laden with the larvae into northern areas (Cowen 1985). Thus, important factors that induce urchins to leave their refuges and overgraze the community include shortage of drift algae, variation in recruitment, and changes in predation pressure (Tegner and Dayton 1991, Dayton et al. 1992). The stability

of kelp–urchin relationships is one of the most interesting questions in kelp ecology (Ehler and Vadas 1990, Tegner and Dayton 1991, Vadas and Steneck 1995) and includes many interrelated environmental factors such as substrate heterogeneity, sea urchin recruitment (influenced by large-scale currents, meso-scale eddies, and by the edge effect of the kelp forest itself), and the nature of the coevolutionary dance between kelps and their grazers.

Predation by fish.—The habitat structure of giant kelp supports several species of small fishes: some graze the kelp fronds directly, whereas others consume invertebrates that settle on the fronds and/or live in the water column around the fronds (North 1971). Both types of predation serve important community roles because some invertebrates, if not controlled by fishes, can consume the kelp forest (Jones 1965, Tegner and Dayton 1987), or they can sink and kill the kelp plants, destroying entire forests (Dayton 1985b). A grazing event that happened after the El Niño, but not after the 1988 storm, probably reflected the relatively long-term absence of the *Macrocyctis* canopy during most of 1983–1984. There were excellent conditions in 1985 for *Macrocyctis* growth and the canopy reformed rapidly. However, an apparent secondary lag effect of the El Niño resulted in the loss of almost two-thirds of the canopy by mid-1985 to dense populations of amphipods, especially *Amphithoe humeralis*. These amphipods are endemic populations normally controlled by small fishes (especially the kelp surf perch, *Brachyistius frenatus*). We speculate that many kelp surf perch were lost with the canopy during the storms; population

recovery of this viviparous, low-fecundity species was slow. This apparently resulted in a dramatic reduction in predation pressure and a release of the amphipods, which, in turn, grazed down the theretofore rapidly recovering kelps. Small fish eventually recruited and were observed with their guts full of amphipods. By late 1985, the amphipod outbreak was over and kelp populations recovered. This is an example of an unexpected lag effect that had massive, if brief, consequences (Tegner and Dayton 1987). A similar grazing event occurred in winter 1965, when the Point Loma canopy was lost between stations >2 km apart (Jones 1965). Thus, the consumption of small grazers and other settling organisms by fishes can have important stabilizing effects on the community.

Finally, another important, but poorly understood biological process is the outbreak of diseases that kill echinoderms. At Point Loma, a disease episode killed almost all of the sea urchins in some 80 ha of barren ground that developed after the 1988 storm (Dayton et al. 1992, Tegner et al. 1995). As at Point Loma, urchin disease in Nova Scotia led to a rebounding of kelp populations (Schiebling 1986). A similar event that killed asteroids throughout much of southern California (Tegner and Dayton 1987, Dayton and Tegner 1990) and the Gulf of California (Dungan et al. 1982) seemed to be associated with the mid-1970 temperature increase (Fig. 2).

ANTHROPOGENIC IMPACTS

Fishing by primitive people

It is often easy to underestimate the importance of primitive people on their ecosystem. The coastal zone of the Northeast Pacific has been subjected to expert hunting for as much as 10 000 years, and Simensted et al. (1978) have demonstrated impressive cascading ecological effects of harvesting sea otters in the Aleutians. In central and southern California, the Chumash Indians had excellent plank boats, and middens show that they took many sea otters as well as large abalones and urchins, prey that would not have been available in the presence of sea otters at their carrying capacity (Dayton and Tegner 1984b). Clearly, this area of California was analogous to that studied by Simensted et al. (1978) in the Aleutians, in that the human harvest of otters apparently released large abalones and sea urchins, which are abundant in middens. Successive waves of European diseases apparently impacted the native people until the mid-1700s, when diseases associated with the Mission system virtually eliminated the native people. It is not known how long sea otters were spared effective native hunts, but when they were harvested in earnest in the late 1700s/early 1800s by Europeans, the otter population apparently had rebounded and was high. Yet, it was virtually eliminated from southern California within a few decades (Reidman and Estes 1988).

Kelp harvest

Macrocystis has been harvested since the turn of the century, but the regulated method of harvest is to cut only the upper 1.2 m of the surface canopy, and this has had no measurable impact at Point Loma (Barilotti et al. 1985). Indeed, although there is considerable interannual variability in yield related to storms and temperature (Tegner et al. 1996a), the long-term stability of the kelp harvest suggests that it may be the best managed harvest of coastal populations in California.

Sewage

Kelp forests near the major metropolitan centers of southern California were devastated by the nearshore discharge of poorly treated sewage in the late 1950s/early 1960s. In the last several decades, however, treatment has improved to the point that there is no measurable impact at Point Loma, and affected kelp forests all over the region have recovered (see references in Tegner and Dayton 1991, Tegner 1993, Tegner et al. 1995). This lack of effect in the short term was demonstrated in 1992, when the San Diego sewage outfall ruptured in the middle of the kelp forest and subjected the community to treated sewage for two months, yet we were not able to identify any important consequence of this accident (Tegner et al. 1995).

Spear fishing

Although southern California is in the northern part of their range (Rosenblatt and Zahuranec 1967), broomtail groupers, *Mycteroperca xenarcha*, and other species of grouper were once common in certain areas (J. Stewart, *personal communication*), and black sea bass (*Stereolepis gigas*) were once plentiful in local kelp forests. These were very large fish weighing hundreds of kilograms. We have no measure of their densities, but old movies, photos, and interviews tell us that it was typical for divers to see several of these fish on one dive. We *guess* that they may have had home ranges of 2–3 ha, suggesting a surprisingly high productivity to feed these large fish. Broomtail groupers are territorial, and we believe that black sea bass tend to remain in home ranges during the spring to fall seasons. Thus, especially for the broomtail groupers, mortality caused by a few spearfishermen may easily explain their loss from the system; black sea bass were also taken by anglers and nets. Equally difficult to quantify is the change in size distributions of hunted species that are still present; historical comparisons of spearfishing contest results with present populations suggest major changes in abundance and size distributions of species such as California sheephead, *Semicossyphus pulcher*. Two decades after the mid 1970s' regime shift, and after gill nets were moved offshore in 1994, a few black sea bass and grouper are reappearing.

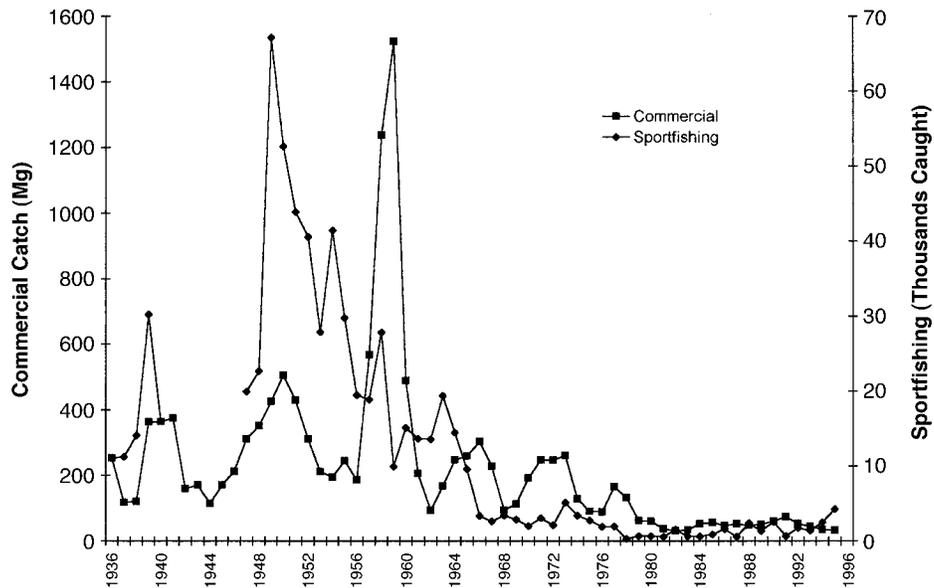


FIG. 4. Commercial and sport (from logbooks of commercial passenger sportfishing vessels) landings of white sea bass (*Atractoscion nobilis*), 1936–1995. There are no sport data available for the years of World War II. Data are compiled from various California Department of Fish and Game sources.

Other sport and commercial fisheries

White seabass (*Atractoscion nobilis*) and yellowtail (*Seriola lalandi*) are two fishes once common along the outer edge of San Diego kelp forests during warm summer months, especially in El Niño years. Divers in the early 1950s observed schools of hundreds of these fishes (J. Stewart, *personal communication*). In extensive diving since 1970, we have never seen more than a half-dozen of either of these species at one time. In the absence of independent stock assessments, the only information available on population size is fishery statistics, and these data are affected by changes in fishing gear, fishing effort, Mexican stocks, markets, and other confounding variables. Yellowtail commercial landings crashed in the mid 1950s and have remained at a few percent of previous landings for the last four decades (Leet et al. 1992). Interpretation of sport and commercial landings of white seabass (Fig. 4) was further complicated by exclusion of U.S. fishermen from Mexican waters in 1982 and the banning of nearshore gill nets in 1994, but landings exhibit a pattern similar to that of yellowtail. An interesting example of reduced expectations can be found in the opinion of some fishery experts that the persistence of this relatively low population during recent years is evidence that the stocks are doing fine, such that they advocate no changes in fishing regulations.

In 1988, a market, primarily the Asian community, was identified for live fishes (California Department of Fish and Game 1996). This fishery focuses on animals that are the size of a single entree (~1 kg), visually attractive, and hardy enough to survive the rigors of capture and transportation. It began with hook and line

gear; after 1989, the use of traps grew rapidly. Target species include California sheephead (*Semicossyphus pulcher*), California halibut (*Paralichthys californianus*), cabezon (*Scorpaenichthys marmoratus*), lingcod (*Ophiodon elongatus*), scorpion fish (*Scorpaena guttata*), and several species of rockfish (*Sebastes* spp.). Statewide, the landings (1 metric ton = 1 Mg) for this fishery jumped over the period 1989 to 1995 from 16 203 to 194 942 Mg for sheephead, 1473 to 115 879 Mg for California halibut, and 163 to 179 785 Mg for cabezon. Some insight into the effects on sheephead populations is offered by Department of Fish and Game logbook data from commercial passenger sport fishing vessels. From 1981 to 1986, an average of 1809 sheephead was taken per year from Point Loma; by 1994–1995, the average number was 145 sheephead/yr. The live-fish fishery has grown as an alternate use of lobster traps in the off-season, and with the prohibition of commercial gill nets within three U.S. nautical miles (5.6 km) of shore in 1994. Essentially, all fishes that respond to bait in a trap are being taken by this fishery, and many of these are now rarely seen. These fisheries are minimally regulated, require inexpensive gear and low effort, and have the potential for virtual elimination of the community roles of these species. The pressure of this fishery on sheephead stocks is especially problematic; these fishes are sequential hermaphrodites and the fishery takes only small females, which may be pre-reproductive (Leet et al. 1992). We have evidence that many of these fishes were once important predators on benthic prey, such as cabezon on abalones (Tegner and Butler 1989), scorpion fish on octopuses (Quast 1968), and sheephead on sea urchins (Tegner and Dayton

1981, Cowen 1983). The changes in sheephead populations suggest that outbreaks of destructive grazing by the minimally exploited purple sea urchin, *Strongylocentrotus purpuratus*, will become more frequent. Natural densities, population size structures, and ecological relationships are unknown for a host of fishes that have functionally disappeared from Point Loma and other coastal kelp forest communities.

Populations of elasmobranchs such as several species of rays and sharks, including gray smoothhounds (*Mustelus californicus*), leopard sharks (*Triakis semifasciata*), and several smaller species, once much more common, were heavily impacted by gill net fishing, whether as target species or as bycatch. Some species have not been seen by our programs since the early 1970s, and all elasmobranchs are now rare. Other species once observed on a regular basis include bat rays (*Myliobatis californica*), torpedo rays (*Torpedo californica*), horn sharks (*Heterodontus francisci*), California halibut, other flat fish, and moray eels (*Gymnothorax mordax*). The elasmobranchs were largely swept from the seas by the gill nets; the halibut and flat fish presumably have been taken by sport and commercial fisheries, including the live-fish fishery. Moray eels, also taken in the live-fish fishery, do not reproduce in California, and their recruitment may be tied to strong El Niño events (McCleneghan 1973); it is not clear whether their absence results from recruitment failure or other ecological factors. Elasmobranchs have very low reproductive rates; although the gill nets have been moved offshore, it is too early to evaluate their recovery. Probably too late to study is the reported relationship between gray smoothhound and leopard sharks that formed large, mixed schools in the early 1950s (Limbaugh 1955; J. Stewart, *personal communication*).

Abalones and spiny lobsters

Both abalones (*Haliotis* spp.) and spiny lobsters (*Panulirus interruptus*) were extremely abundant before diving and effective trap fisheries. Again, there are no data on former abundance, but Chinese immigrants in the San Diego region, working intertidally and in the shallow subtidal with poles and gaffs, landed 1.86×10^6 kg (4.1 million pounds) in 1879 alone (Cox 1962). Divers of the 1950s reported green abalones stacked on top of each other in shallow water and describe the Point Loma kelp forest as "paved with red abalones" (J. Stewart, *personal communication*). Abalones are now so scarce that all five species fished in southern California have been closed to both sport and commercial harvest, and there is good reason to believe that one, *H. sorenseni*, will become the first marine invertebrate known to become biologically extinct as a result of human fishing (Tegner et al. 1996b).

Probably because the spiny lobster source population has yet to be rendered ecologically extinct in Mexico,

the lobster fishery has persisted, but abundance and size distributions are clearly different from historical patterns. The commercial fishery began in 1872, and in 1887 the average lobster taken was ~150 mm in carapace length (CL). By 1955, the average lobster from the commercial fishery was ~119 mm CL. Average harvest in San Diego from 1976 to 1980 varied from 86 mm to 90 mm CL. In 1888, 260 traps yielded 104 807 kg (231 060 pounds) of lobsters. By 1975, 19 000 traps were required to harvest almost the same mass, 105 768 kg (233 179 pounds; see references in Tegner and Levin 1983). Lobster landings, although well below the peaks of the 1950s, have continued through the mid-1990s at relatively high levels in comparison with other fisheries. Nevertheless, because larger lobsters have higher feeding rates and consume larger sea urchin prey (Tegner and Levin 1983), their functional role in the kelp forest today is very different from that apparent at the turn of the century.

Sea urchins and other invertebrates

Before the fishery for red sea urchins, *Strongylocentrotus franciscanus*, grew to full strength in the mid-1970s at Point Loma, the target species was common throughout the forest (Tegner and Dayton 1981). By the late 1980s, this urchin remained abundant along the outer edge of the forest, but was functionally absent from much of the interior (Tegner and Dayton 1991). Besides their well-known potential for overgrazing kelps, red urchins have positive impacts on the community. The spine canopy association of species that shelter under adult sea urchins is an important recruitment habitat for abalones and urchins (Tegner and Dayton 1977, Tegner and Butler 1989), and its competitive interactions with its congener, *S. purpuratus*, may be important for controlling the distribution of the smaller echinoid (Schroeter 1978). Recruitment is maintaining red sea urchin populations along the outer edge of the forest, but recruitment decreases with distance into the forest and is virtually zero along the inner margin (Tegner and Dayton 1991).

Unregulated commercial fisheries have recently targeted invertebrates such as holothurians (10 454 kg were landed in San Diego in 1995) and snails. Some snails are not identified in the records, but presumably include *Lithopoma*: 1590 kg were landed in San Diego in 1995. Others such as *Kellettia* reproduce in large aggregations (Rosenthal 1971) and are particularly vulnerable to unregulated take; >900 kg were identified as landed in San Diego in 1995. Only a few samples of their densities before the fishery commenced exist, and these animals may now be joining the sequential depletion of fishable stocks.

Asteroids are not exploited, but their populations also decreased substantially between 1972 and the early 1980s (Fig. 5). Two species that were abundant in 1972 have shown no evidence of recovery, whereas a third

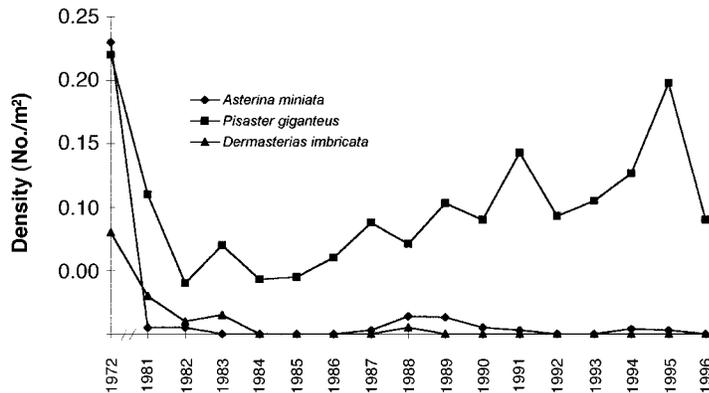


FIG. 5. Asteroid densities from the 15-m site in the center of the Point Loma kelp forest, 1972–1996.

has been increasing in abundance since the early 1980s. *Asterina miniata* populations were decimated by disease episodes associated with warm water in 1978 and 1983 (Tegner and Dayton 1987); although not well documented, this disease also affected other asteroids. *Asterina miniata* appears to control populations of white sea urchins (*Lytechinus anameus*), whereas *Dermasterias imbricata* preys on purple sea urchins (see references in Tegner and Dayton 1987). The association of the disease with warmer water and the higher abundance of these asteroids in colder, deeper water (*unpublished data*) are consistent with their disappearance being related to the oceanographic climate shift in the mid-1970s.

DISCUSSION

The role of interannual oceanographic variability is rarely considered in the large benthic ecology literature on disturbance and subsequent succession (Tegner et al. 1997). Most benthic research focuses on recruitment processes and biological interactions, and much of the theory focuses on attributes of disturbance regimes (extent, intensity, frequency, periodicity) as they affect patches, colonization, succession, and community stability. In contrast with pelagic systems, which are widely appreciated to be driven by physical processes, large-scale oceanographic variability and its effects on benthic systems are rarely considered and poorly understood.

Most oceanographers realize the role of physical forcing in interannual variability and, because of the fluid nature of the ecosystem, most biological oceanographic research is tightly coupled with physics. Furthermore, the mechanics of physical forcing in long-term variability are becoming clearer. For example, El Niños, described long ago off of South America, are now better understood in extratropical regions (Chelton et al. 1982). El Niños persist for up to three years, but longer term oceanographic shifts are well described, even in McMurdo Sound, Antarctica, in which approximate decadal changes in water column ice formation, or the lack of it, forced major benthic changes

with probable long-term lag effects in the shallow benthic community (Dayton 1989). Another example is the “Russell Cycle,” which refers to a multidecadal shift in water masses in the English Channel (Steele 1996). Barry et al. (1995) resurveyed permanent quadrats in a central California intertidal habitat and found a significant shift of species, with colder water distributions being replaced by those with warm-water affinities since the 1930s. Perhaps the most important long-term change in oceanographic trends that *may* relate to global warming is the recent report of a 70% decline in zooplankton over the last 40 years in two regions of the California Current (Roemmich and McGowan 1995). The proximal cause of this shift is believed to be slightly warmer surface water, which acts to stabilize and deepen the thermocline, resulting in less mixing of deep, nutrient-rich water. Our *Macrocystis* stipe data showing important changes between the ocean climate in the 1950s and early 1970s and the 1980s certainly are consistent with the larger scale California Current picture, and support a regime shift in the mid-to-late 1970s. Hayward (1997) has collected tantalizing data from five different pelagic ecosystems of the Pacific Ocean that all suggest regime shifts starting in the mid-1970s.

Like most other marine ecosystems, the kelp forest is marked by a great deal of natural variation. Given a stratified design to account for known or suspected gradients, there are still many sources of variation that would very likely confuse a monitoring program not based on sophisticated, mechanistic understanding and long-term data. Clearly, the recent history of the community is critical for understanding patterns at any point in time. Here, we have a good understanding of the mechanisms affecting the kelps and can make predictions of community consequences of various types of disturbances, but there are so many sources of variation, both regionally and within sites, that detecting trends with statistical methods is very difficult. In terms of the megafauna of kelp forests, the baseline had shifted considerably before the ecological roles of most of

these species could be studied and, in many cases, even before fishery-dependent data were collected. Available data on the ghosts of once-abundant species are scarce, of limited value, or anecdotal; in many cases, application of commonly accepted statistical bases for validating decisions may be impossible.

Anthropogenic alteration of most environmental systems occurs via an accumulation of impacts, large and small. Ecologists have not devised good means of evaluating cumulative effects, and a better measure of evaluating community dynamics is necessary to search for system stress. Despite the existence of keystone effects in some systems (Paine 1994), most systems do not collapse with the functional or ecological loss of species, they just become more depauperate and lower in biodiversity, and people rarely notice. Sea otters have been cited as a keystone species in kelp forest communities for their impact on urchin populations, yet large giant kelp populations have characterized southern California for more than a century after otters were hunted out (Foster and Schiel 1988, Foster 1990), and now the large red urchin fishery has greatly reduced the potential for overgrazing throughout its range (Tegner and Dayton 1991). All continental-shelf ecosystems have lost many species, in the sense that populations have been reduced so low that they can not exert former ecological roles and often are never seen (Dayton et al. 1995, Vadas and Steneck 1995, Witman and Sebens 1992). We note, however, that the differences in kelp and urchin abundance patterns in the Gulf of Maine with distance offshore strongly suggest that functional changes have occurred there (Vadas and Steneck 1995, Witman and Sebens 1992). Similarly, many pelagic systems have lost most of their tuna, cod, whales, turtles, elasmobranchs, etc., yet they have not collapsed and, with the exception of the whale-krill relationship, there may be no *known* (not to imply that they do not exist) ecosystem consequences. The enigma is that even if such species are not biologically extinct, certainly they are ecologically extinct, yet the systems continue to function without them. It is very important to recognize their absence, even though the systems persist.

In addition to exploitation of target species, many fisheries exert huge environmental impacts on other species in the habitat (Dayton et al. 1995). Bycatch is perhaps the most serious general environmental consequence of fishing. This incidental take of active fishing gear results in the ecological extinction (almost complete removal of the species) of virtually all air-breathing marine species (mammals, reptiles, and birds), as well as many, if not most, species of elasmobranchs and other long-lived organisms that are killed as a consequence of accidental take. In addition to the effects of active fishing gear is the virtually unknown, but very serious, problem resulting from the loss of gear that continues to fish. These losses can

include 20–40% of the gear annually, and much of this debris continues to fish for years. This problem is completely out of sight and rarely addressed, but has massive consequences.

Most ground fisheries destroy natural benthic communities by killing many small individuals of the target species and most epibenthic species (many of which are important nurseries or food sources for other species), and by disturbing the substratum enough that the community becomes colonized by species that can live in such heavily disturbed habitats (Dayton et al. 1995, Auster et al. 1996). Note that the benthos does not become azoic; rather, it develops a completely different association of deposit feeders that have high turnover potential and may resist recovery of the natural populations. In addition to mortality of the bycaught species, there are sometimes important secondary effects of their discard, such as large-scale oxygen depletion, diseases, and the enhancement of selected species of seabirds that, in turn, impact other populations.

Our point here is that, in most marine examples, the indirect effects of reductions of so many species are completely unknown because there are no baseline data for comparison. Yet, the selective removal of so many organisms and so much biomass must have significant consequences; one thinks about the loss of large populations of king crabs and lobsters in both hemispheres, the huge fish of coral reefs, populations of manatees and turtles dense enough to physically stop the ships of Columbus' second expedition (Jackson 1997), and all the mammals (almost 1×10^6 Mg, or a million tons of whales from the Gulf of Maine alone), which surely had important impacts on their systems (Dayton et al. 1995).

We return to the challenge of identifying major regime shifts and differentiating these from anthropogenic disturbances. It is virtually impossible to make such a distinction without some form of benchmark criteria of "normal." In terrestrial situations, there are usually parks, wilderness areas, and other means of at least developing a general idea of what a natural habitat might look like. However, we have almost no such insights for marine systems. We have a sliding and continually reduced expectation or concept of what the natural system should be. It is as though one attempted to recreate a rain forest or tall-grass prairie when all we have ever known is horizon-to-horizon corn or wheat fields, or, more appropriately, strip-mined areas unable to recover for lack of seed sources and recruitment habitats. This is not an exaggeration: many of the most productive continental-shelf habitats in the world are dredged and dragged several times per year. In many cases, the natural community originally had a great deal of biogenic structure contributed by slow-growing, long-lived species such as sponges and bryozoa, species with low dispersal and reproductive rates and very slow recovery potential. Such structure once

furnished nursery habitats for recruitment (Dayton et al. 1995, Auster et al. 1996). In other situations, dredging has drastically reduced populations of large, slow-growing, and long-lived bivalves (Thrush et al. 1995). Most marine problems are so severe that it may be a waste of time to develop sophisticated statistics, because there are virtually no appropriate benchmark data describing a natural standard. We desperately need to establish meaningful reserves and to adopt more conservative policies for fisheries management.

The basic issue is how to evaluate anthropogenic effects on benthic habitats along the continental shelf in relation to natural short-term variability and longer term oceanographic regime shifts. First, one needs to have some measure of natural variability. In the larger sense that the benthic community is tied to the productivity of the water column above it, what sort of long-term data are available to evaluate pelagic events? The CalCOFI (California Cooperative Oceanic Fisheries Investigations) program is the only large-scale, long-term program evaluating such questions in the world, and it has documented a 70% reduction in zooplankton biomass over the last 40 yr (Roemmich and McGowan 1995). It is hard to know how this affects the entire benthic community, but it was difficult to show benthic impacts of short-term ENSO effects (Dayton and Tegner 1990). We have shown that this change in the oceanographic climate did affect *Macrocystis*, and that one can measure *Macrocystis* impacts on understory kelp (Tegner et al. 1996a, 1997). More problematic is the role of climate change in the depletion of stocks taken by fisheries; regime shifts are well known for their impacts on the abundance of some fish populations in the California Current (McCall 1996). Increasing temperatures since the 1970s could have contributed to the decline of northerly kelp forest species such as lingcod, but we note that the last abalone species open to fishing in southern California was the red (*Haliotis rufescens*) abalone, a colder water species.

CONCLUSIONS

The value of long-term data is axiomatic for ecologists. We have presented many examples of insights from such data for detecting trends in kelp populations within a large kelp forest. As with other trend analyses, rare climatological vagaries at all scales can have important, far-reaching effects on trends, and the best tactic for understanding the implications of climatic variables may be reliance on a mechanistic understanding of the physical and biological processes structuring the kelp community. The most important message of this paper is that, no matter how well one understands kelp populations, any current program will fail to discern the ghosts of missing animals. That is, any biologist studying the community now will see interesting biology of kelp and small animals, but the expectations of what is natural are much reduced and are likely to

be an inappropriate basis for making fisheries and environmental decisions. It would be similar to studying the Serengeti after all the large grazers and carnivores were eliminated; one could still appreciate termites and other small grazers, but one's expectations of nature pale beside what it used to be. Here, we may understand the kelps; however, they are but a beautiful gossamer veil, undulating peacefully in the ocean, offering no hints of the marvelous species that should live there but for human greed.

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