

Kelp forest ecosystems: biodiversity, stability, resilience and future

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SUMMARY

Kelp forests are phylogenetically diverse, structurally complex and highly productive components of cold-water rocky marine coastlines. This paper reviews the conditions in which kelp forests develop globally and where, why and at what rate they become deforested. The ecology and long archaeological history of kelp forests are examined through case studies from southern California, the Aleutian Islands and the western North Atlantic, well-studied locations that represent the widest possible range in kelp forest biodiversity. Global distribution of kelp forests is physiologically constrained by light at high latitudes and by nutrients, warm temperatures and other macrophytes at low latitudes. Within mid-latitude belts (roughly 40–60° latitude in both hemispheres) well-developed kelp forests are most threatened by herbivory, usually from sea urchins. Overfishing and extirpation of highly valued vertebrate apex predators often triggered herbivore population increases, leading to widespread kelp deforestation. Such deforestations have the most profound and lasting impacts on species-depauperate systems, such as those in Alaska and the western North Atlantic. Globally urchin-induced deforestation has been increasing over the past 2–3 decades. Continued fishing down of coastal food webs has resulted in shifting harvesting targets from apex predators to their invertebrate prey, including kelp-grazing herbivores. The recent global expansion of sea urchin harvesting has led to the widespread extirpation of this herbivore, and kelp forests have returned in some locations but, for the first time, these forests are devoid of vertebrate apex predators. In the western North Atlantic, large predatory crabs have recently filled this void and they have become the new apex predator in this system. Similar shifts from fish- to crab-dominance may have occurred in coastal zones of the United Kingdom and Japan, where large predatory finfish were extirpated long ago. Three

North American case studies of kelp forests were examined to determine their long history with humans and project the status of future kelp forests to the year 2025. Fishing impacts on kelp forest systems have been both profound and much longer in duration than previously thought. Archaeological data suggest that coastal peoples exploited kelp forest organisms for thousands of years, occasionally resulting in localized losses of apex predators, outbreaks of sea urchin populations and probably small-scale deforestation. Over the past two centuries, commercial exploitation for export led to the extirpation of sea urchin predators, such as the sea otter in the North Pacific and predatory fishes like the cod in the North Atlantic. The large-scale removal of predators for export markets increased sea urchin abundances and promoted the decline of kelp forests over vast areas. Despite southern California having one of the longest known associations with coastal kelp forests, widespread deforestation is rare. It is possible that functional redundancies among predators and herbivores make this most diverse system most stable. Such biodiverse kelp forests may also resist invasion from non-native species. In the species-depauperate western North Atlantic, introduced algal competitors carpet the benthos and threaten future kelp dominance. There, other non-native herbivores and predators have become established and dominant components of this system. Climate changes have had measurable impacts on kelp forest ecosystems and efforts to control the emission of greenhouse gases should be a global priority. However, overfishing appears to be the greatest manageable threat to kelp forest ecosystems over the 2025 time horizon. Management should focus on minimizing fishing impacts and restoring populations of functionally important species in these systems.

Keywords: apex predators, biodiversity, herbivory, human interactions, kelp forests, trophic cascades

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INTRODUCTION

'I can only compare these great aquatic forests ... with the terrestrial ones in the intertropical regions. Yet if in any country a forest was destroyed, I do not believe nearly so many species of animals would perish as would here, from the destruction of the kelp. Amidst the leaves of this plant numerous species of fish live, which nowhere else could find food or shelter; with their destruction the many cormorants and other fishing birds, the otters, seals, and porpoise, would soon perish also; and lastly, the Fuegian[s] ... would ... decrease in numbers and perhaps cease to exist.'

Charles Darwin, 1 June 1834, Tierra del Fuego, Chile (Darwin 1909, pp. 256–257).

Kelp forests dominate shallow rocky coasts of the world's cold-water marine habitats. They comprise primarily brown algae in the order Laminariales and produce the largest biogenic structures found in benthic marine systems (Dayton 1985a). Kelp forest ecosystems include structure-producing kelps and their myriad associated biota such as marine mammals, fishes, crabs, sea urchins, molluscs, other algae and epibiota that collectively make this one of the most diverse and productive ecosystems of the world (Mann 1973). Economically, kelp forest ecosystems have been significant to maritime peoples for thousands of years (Simenstad *et al.* 1978; Erlandson 2001).

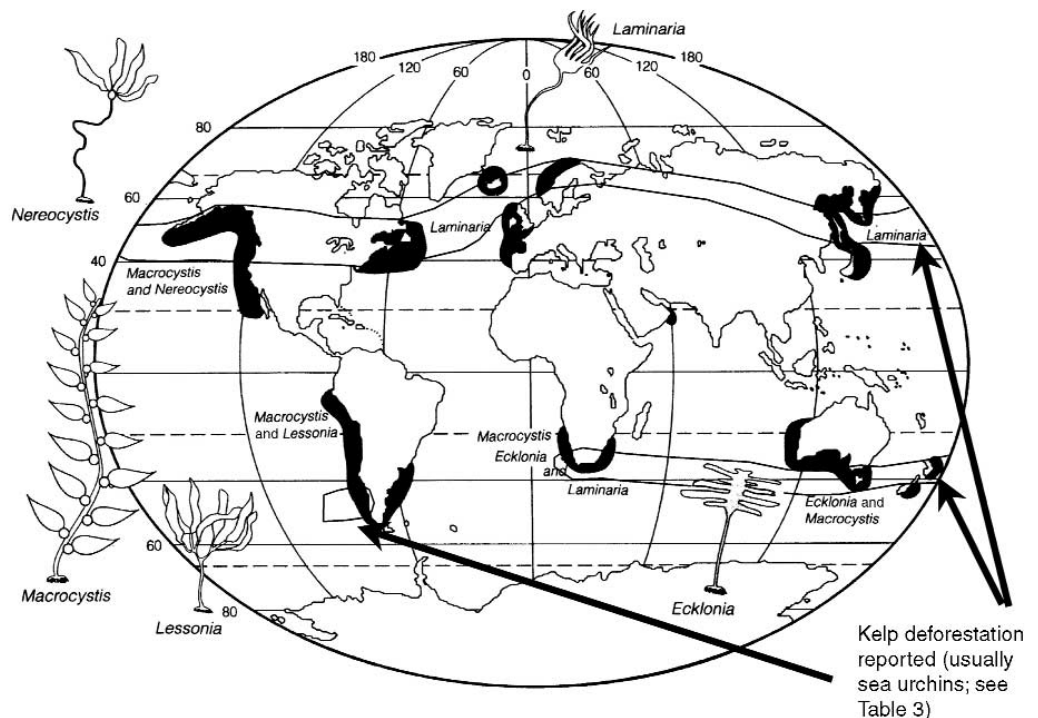
Past reviews provided contemporary overviews of kelp forests (Kain 1979; Dayton 1985a; Schiel & Foster 1986; Witman & Dayton 2001). These rarely considered how kelp forest ecosystems have changed at very large spatial scales

over very long periods of time spanning decades to millennia (Jackson *et al.* 2001). A longer historical perspective allows us to see how kelp forest ecosystems have changed and possibly where they are headed in the future. Thus, it is with larger spatial and temporal perspective that we embarked on this review.

The nature of kelp

Three morphological groups or 'guilds' of kelp are defined by the canopy height of their fronds (Dayton 1985a). 'Canopy' kelps are largest and produce floating canopies. Chief among these is the giant kelp, *Macrocystis* spp. which grows to 45 m long (Abbott & Hollenberg 1976) and dominates kelp forests along the west coasts of North and South America and at scattered locations in the South Pacific Ocean including South Africa, southern Australia, New Zealand and several subantarctic islands (Fig. 1). Smaller canopy kelps include *Nereocystis leutkeana*, which ranges from Central California to Alaska, and its Southern Hemisphere counterpart, *Ecklonia maxima* in South Africa, and *Alaria fistulosa* in Alaska and the Pacific coast of Asia. These kelps reach about 10 m in length. 'Stipitate' kelp fronds are held above the benthos with rigid stipes (Dayton 1985a). They include some species of *Laminaria* sp. in Europe and the Pacific Northwest, *Ecklonia* in southern Australia and New Zealand, and *Lessonia* in Chile. Stipitate *Laminaria* dominates kelp forests of the North Pacific from Japan, north-east across coastal Alaska to northern California. Most species of *Laminaria* are less than 5 m long, but a few grow to 10 m in length. Other stipitate genera found along the Pacific coast of North America include *Pterygophora*, *Eisenia*, *Pleurophyucus* and

Figure 1 Kelp forest distributions of the world and their dominant genera (from Raffaelli & Hawkins 1996).



Thalassiophyllum. 'Prostrate' kelps are most diminutive and cover the benthos with their fronds. This guild includes several species of *Laminaria*, which dominate most of the Northern Hemisphere except for parts of the eastern North Pacific (Fig. 1). Prostrate *Laminaria* forests range from the Gulf of Maine to Greenland in the western North Atlantic and from Iceland to the high Arctic of Norway and south to the north-westernmost corner of Africa, in the eastern North Atlantic. Taxonomically, the kelps themselves are not diverse. The most diverse kelp flora occurs along the California coast of North America. However, it only has 20 species of kelp distributed among 16 genera because most genera are monotypic (Abbott & Hollenberg 1976).

Despite their low taxonomic diversity, kelps are highly diverse structurally and functionally. They possess specialized cells for translocation (for example, 'trumpet hyphae' and sieve elements) that allow them to attain their great size and diverse morphology. Even within species, developmental stages and ploidy-phases of kelp span an unparalleled range of sizes and shapes. Their gametophyte stage is an inconspicuous, microscopic filament living within the benthic boundary layer (Neushul 1972). In this microhabitat fertilization occurs and developing sporophytes grow. Depending on the adult morphology of the species, the kelp fronds may remain near the benthos (prostrate forms), occupy intermediate depths (stipitate forms), or grow to and float on the surface (canopy forms) (Neushul 1972). Morphology varies widely among and within genera. The tiering of kelp morphologies along with other associated taxa contributes to the structural diversity of this system. All three kelp forms can coexist (Dayton 1985a) together with a patchy carpet of corticated macrophyte turf (Dayton 1975) and a pavement of encrusting coralline algae. Each of these structural components is habitat and food for associated organisms. Thus the unique anatomy of kelp allows communities to attain the stature of forests with wide-ranging implications for associated organisms and coastal communities.

The structure and function of kelp forests differ significantly from their terrestrial counterparts dominated by angiosperm and gymnosperm trees. Compared to terrestrial forests, kelp forests are more productive and diverse (at the phyla level), but the average lifespan and structural height is less. For example, many mature terrestrial forests attain canopy heights of 10–30 m within 20 to 30 years. Individual trees can have longevities of centuries to millennia. Associated with terrestrial forests are animals primarily from the three phyla Chordata, Arthropoda and Annelida. In contrast, kelp forests reach canopy heights of 1–15 m (although *Macrocystis* is larger than this) within 1–3 years. Individual kelps have maximum longevities of about 25 years (Steneck & Dethier 1994). Associated with kelp forests are animals from more than 10 phyla, namely Chordata, Arthropoda, Annelida, Echinodermata, Bryozoa, Cnidaria, Mollusca, Platyhelminthes, Brachiopoda and Porifera.

The physical structure, algal biomass and organisms associated with kelp forests profoundly alter local environ-

ments and ecologies. Kelp canopies dampen waves, which influence water flow and associated processes of coastal erosion, sedimentation, benthic productivity (primary and secondary) and recruitment (Duggins *et al.* 1990). The canopies also reduce light, creating understory conditions favourable for a suite of species adapted to low light intensity (Santelices & Ojeda 1984a); as a result, they can influence interspecific competition among algae (Dayton 1985a). Kelps are substratum for numerous sessile animals and algae (Duggins 1980; Reed & Foster 1984; Dunton & Shell 1987) and habitat for mobile organisms specialized to live and feed directly on the kelp or its associated assemblages. For example, trophically specialized limpets depend upon kelp for their existence (Steneck & Watling 1982; Estes & Steinberg 1988; Bustamante *et al.* 1995). Kelp forest architecture provides habitat, nursery ground and food for myriad mobile pelagic and benthic organisms (Bernstein & Jung 1980; Bologna & Steneck 1993; Levin 1994; Anderson *et al.* 1997). Since predatory fishes use canopies as habitat, canopy loss can translate to increased survivorship of resident prey organisms and their larvae (Gaines & Roughgarden 1987). Thus, as kelp canopies vary, the ecological and oceanographic processes associated with them will be altered.

Kelps concentrate biomass and are a significant source of nutrition for coastal marine ecosystems via food webs based on macroalgal detritus (Duggins *et al.* 1989) because herbivores rarely consume more than 10% of the living biomass (Mann 2000). Large pieces of kelp commonly litter the benthos in coastal zones and become food for detritivores and microbes (Linley *et al.* 1981), thus making their carbon available to the coastal community of suspension feeders as well as the herbivores and detritivores feeding directly on kelps (Dunton & Schell 1987; Duggins *et al.* 1989). In effect, kelp forests concentrate and magnify secondary production, thereby supporting complex food webs in coastal zones (Duggins *et al.* 1989; Mann 2000).

The combination of high kelp productivity in environments with the potential for high rates of disturbance can make these forests surprisingly ephemeral. Entire kelp beds can be eliminated by thermal events, storms or outbreaks of herbivores and disappear without a trace within a year, but significantly, the entire community can return nearly as quickly (Scheibling 1984; Harrold & Reed 1985; Hart & Scheibling 1988; Witman 1988; Tegner *et al.* 1997).

As with most ecosystems, kelp forests are strongly influenced by both their physical and biological environment. Fortunately, we know much more about how environmental forcing functions operate in kelp forests than we do for most other ecosystems. Kelp forests are ideally located and scaled for human study; most components of the system are readily observable, kelp forest phase-changes are rapid (i.e. occurring within a few years) and manipulative experiments of canopy removal or transplantation are easily accomplished. Thus, hypotheses can be advanced, tested, reported and challenged within a decade.

LARGE SCALE PATTERNS: GLOBAL INTERPLAY OF DIVERSITY, PRODUCTIVITY AND DISTURBANCE

The ecology of kelp forests

Kelp forests persist in a balance between ecological processes driving their development and their deforestation. They wax as a result of recruitment and net productivity and wane as a result of biomass lost from disturbances both physical and biological and competition. These factors are influenced by properties intrinsic to, and extrinsic of, the kelp (Steneck & Dethier 1994). Complex, multifactorial interactions make long-term changes in these systems difficult to demonstrate and predict (Tegner *et al.* 1996a). Further, the population density and community development in structurally diverse (high canopy) kelp forests may decouple changes in the canopy cover from changes in population densities, thus obscuring linkages between patterns and processes (Schiel & Foster 1986; Dayton *et al.* 1998). Nevertheless, several strong ecological interactions control forest development and deforestation. These operate at varying spatial and temporal scales and they will be the focus of this section. For this, we will consider where kelps can live, where they develop forests, and under what conditions kelp deforestation takes place.

Kelp forest development

Globally, kelp forests develop on shallow rocky shores in a mid-latitude band where light and oceanographic conditions allow the development and persistence of this growth form (Fig. 1). While kelps can grow in Arctic and sub-Antarctic regions (see Dunton & Dayton 1995), their abundance and diversity are low (probably due to light limitations; Dunton 1990; Henley & Dunton 1997) and thus they rarely develop forests above about 60° latitude. Similarly, warm temperatures and low nutrient concentrations generally prevent kelp forests from developing in subtropical or tropical regions (Bolton & Anderson 1987; Gerard 1997). The lowest latitude kelp beds (see Hatcher *et al.* 1987) usually correspond with ocean current driven anomalies in latitudinal gradients of warm temperatures and/or low nutrient conditions. For example, kelp forests are found within the tropics of Cancer and Capricorn only along the western coasts of southern California to Mexico, northern Chile to Peru, western South Africa and western Australia (Fig. 1). In these cases, cool ocean currents flowing toward the equator, or upwelling, advect cool, nutrient-rich water to the kelp forests.

Low latitude kelp (usually less than 40° latitude) are often diminutive and share or lose community dominance to fucoids such as *Sargassum* and other large brown algae that become more diverse and abundant toward the tropics. In North America, southern California kelps share space with the fucoids *Cystoseira osmundacea* (40–30° N latitude) and *Sargassum* spp. (35–25° N latitude) (Foster & Schiel 1985). At Japan's southern island, Honshu, scores of *Sargassum* species become increasingly important and eventually dominate macroalgal communities at latitudes less than about

40° N (Fujita 1998). One of the northernmost kelp of the Southern Hemisphere is in Western Australia at 28–29° S latitude (Hatcher *et al.* 1987), where diminutive *Ecklonia* share space with brown algal species of *Lobophora* and *Sargassum*. Elsewhere in South Australia (Shepherd & Womersley 1970) and New Zealand (Choat & Schiel 1982), large subtidal fucoids cohabit with and often dominate the kelp. In New Zealand, fucoid densities were twice that of kelp densities at low latitude (<40° S) sites, but reversed to kelp dominance at the higher latitude site (>40° S), where kelp densities were twice that of the fucoids (Choat & Schiel 1982). New Zealand fucoids frequently dominate shallow zones (upper 5 m), displacing kelp dominance to below 10 m (Choat & Schiel 1982). Only the relatively low diversity kelp forests of South Africa (22–35° S latitude) and northern Chile (40–20° S latitude) are without fucoids (Bolton 1996). However, in Chile the large kelp-like *Durvillaea* sp. (closely related to the fucoids) commonly dominates shallow zones (Santelices 1990) and may outcompete *Macrocystis* there (Dayton 1985b).

In general, the three interacting processes that control the development of kelp forests are recruitment, growth and competition. Locally, kelp forests are established and maintained by successful settlement of zygotes, which grow and are thinned by mortality from intraspecific competition during their benthic life (Reed & Foster 1984; Chapman 1986). Recruitment is often seasonal and influenced by environmental conditions at the time of settlement. In complex kelp forests tiered with multiple levels (for example, canopy, stipitate and prostrate forms; Table 1) such as the California kelp forest, kelp recruitment and growth is regulated by light available through breaks in the kelp canopy (Reed & Foster 1984; Santelices & Ojeda 1984a; Graham *et al.* 1997) as well as by available nutrients (Dayton *et al.* 1999). Following intense storms that deforest or thin kelp canopies, recruitment is usually strong, but the kelp species that grow to dominance will depend upon nutrient conditions at the time (Tegner *et al.* 1997).

Kelp growth depends on interactions among nutrient availability, temperature and light. Kelps dominate cold-water coastal zones (Fig. 1) but can become physiologically stressed at high sea temperatures, particularly when nutrient availability is low (Tegner *et al.* 1996a; Gerard 1997). In some regions without upwelling, periods of low nutrient concentrations correspond with warm summer temperatures when the water is stratified. The combined effects of low nutrients and high rates of respiration result in kelp plants that erode more rapidly than they grow (Gagne *et al.* 1982; R.S. Steneck, unpublished data 2002). In kelp forests driven by the upwelling of new nitrogen, such as those of southern California, warm surface water temperature is a surrogate for low nutrient availability (Tegner *et al.* 1996a). In this system when El Niño events disrupt coastal upwelling, kelp becomes nutrient-starved and dies back (Tegner & Dayton 1991). As a result, the distribution, abundance and size of kelp plants decline as sea surface temperatures increase (Dayton *et al.* 1999).

Table 1 Dominant organisms, functional groups and diversity that define the structure and function of subtidal kelp forest ecosystems of North America. *Steller's sea cow (now extinct).

	<i>Western North Atlantic</i>	<i>Aleutians, Alaska</i>	<i>Southern California</i>
<i>Dominant kelp genera</i>	<i>Laminaria</i> (1 sp.), <i>Agarum</i> (1 sp.)	<i>Alaria</i> (1 sp.), <i>Laminaria</i> (3 spp.), <i>Thalassiophyllum</i> (1 sp.), <i>Agarum</i> (1 sp.)	<i>Macrocystis</i> (1 sp.), <i>Pterygophora</i> (1 sp.), <i>Laminaria</i> (1 sp.), <i>Eisenia</i> (1 sp.), <i>Pelagophycus</i> (1 sp.), <i>Egregia</i> (1 sp.), <i>Agarum</i> (1 sp.)
<i>Structural tiering</i> (<i>kelp guilds</i>)	Prostrate	Canopy, stipitate, prostrate	Canopy, stipitate, prostrate
<i>Dominant herbivores</i>			
Sea urchins	<i>Strongylocentrotus droebachiensis</i>	<i>Strongylocentrotus polycanthus</i>	<i>Lytechinus anamesus</i> , <i>Strongylocentrotus purpuratus</i> , <i>S. franciscanus</i>
Molluscs			<i>Haliotis</i> (3 spp.), <i>Tegula</i> (3 spp.)
Fishes			<i>Medialuna californiensis</i> , <i>Girella</i> <i>nigricanus</i>
Marine mammals		<i>Hydrodamalis gigas</i> *	<i>Hydrodamalis gigas</i> *
<i>Dominant carnivores</i>	Atlantic cod (<i>Gadhus morhua</i>)	Sea otter (<i>Enhydra lutris</i>), killer whales (<i>Orcinus orca</i>)	Sea otter, spiny lobster (<i>Panulirus</i> <i>interruptus</i>), sheephead fish (<i>Semicossyphus pulcher</i>)

As a group, kelps have a relatively low photosynthetic to biomass ratio. This constrains them to relatively shallow, well-illuminated zones compared to other functional groups of algae (reviewed in Vadas & Steneck 1988). In environments free of herbivores or other agents of disturbance, kelp frond size and density decline rapidly with depth making kelps the shallowest of the major growth forms of marine algae (Steneck & Dethier 1994). Extended periods of darkness in the Arctic limit the northern distribution (Fig. 1), diversity and maximum depth of kelps (Henley & Dunton 1997).

The limited development of kelps at high latitudes results from interactions among light, temperature, ice scour, nutrients and evolutionary biogeography. As a result, true kelps (order Laminariales) grow much further north in the Arctic (to about 70° North latitude) than they do south in the Antarctic (to 55° South latitude) (Dunton & Dayton 1995). Kelp growth in near-freezing seawater temperatures requires dissolved inorganic nitrogen to physiologically accommodate photosynthesis (Korb & Gerard 2000). The endemic Arctic kelp *Laminaria solidungula* has a remarkable capacity to store nitrogen that is only available in the winter when it has no light (Henley & Dunton 1997). In contrast, in the Antarctic where nitrogen is available all year round, true kelps are displaced by morphologically similar brown algae, *Himantothallus* sp. of the order Desmarestiales (Moe & Silva 1981; Dunton & Dayton 1995). This kelp-like alga has no inherent capacity to store nitrogen, nor does it need to in the nitrogen-replete waters of the Antarctic. Under experimental nitrogen-starved conditions this alga quickly succumbs (Korb & Gerard 2000). Thus Arctic and Antarctic distributions of kelp may hinge on physiological adaptations to light and nutrient limitations in those areas. Arctic kelp illustrates the remarkable range of physiological tolerance that can evolve in the group. The effective replacement of

Laminariales in the high Antarctic by large brown algae in the order Desmarestiales may be an evolutionary priority effect of an older order in the geologically older Southern Hemisphere ocean system. Nevertheless, polar populations of kelps or kelp growth forms may grow to their physiological limits at high latitudes but they do not attain forest there. Seasonal change in oceanography and physical disturbances from ice scour can limit or eliminate subarctic populations of kelps (Himmelman 1980).

Kelp deforestation

Widespread kelp deforestation can result from disease, herbivory, and physiological stress or interactions among those processes. At lower latitude kelp forests (usually less than 40°), periodic deforestations results from oceanographic anomalies in temperature, salinity or nutrients that either kill kelps directly or trigger diseases that become lethal to physiologically-stressed plants. At mid-latitudes (about 40–60°), herbivory by sea urchins is the most common and most important agent of kelp deforestation. Latitudinal differences in patterns and processes shaping kelp forests have resulted in different researchers working in the same kelp forest system but reaching different conclusions (Foster 1990). Here we address the geography of kelp deforestation patterns and processes.

Kelp-free patches have probably always occurred at some scale but those created by physical factors tend to be relatively small and short-lived. The oldest term for algal deforestation is the Japanese word *isoyake*, which means 'rock burning' (D. Fujita, personal communication 2002). The word was coined by Yendo (1902, 1903) to describe algal deforestation in coastal zones of central Japan where the algal decline was thought to have resulted from salinity anomalies (Yendo 1903, 1914) rather than grazing, because herbivorous

sea urchins were rare. The isoyake killed all foliaceous algae first and then all encrusting coralline algae; the algae recovered several years later (Yendo 1914). Other mass mortalities of *Ecklonia*- and *Eisenia*-dominated kelp forests resulted from incursions of the Kuroshio Current along the central Japan coast (D. Fujita, personal communication 2002). On Honshu Island, near the southern limit of Japanese kelp, anomalous incursions of the warm Tsushima Current periodically create isoyake conditions. Such oceanographically-induced kelp deforestations are usually short-lived and reversible, as was the original isoyake case in Japan (Yendo 1914).

Kelp deforestations also result from El Niño events. Strong El Niños halt coastal upwelling of nutrient-rich water and cause surface waters to warm (Dayton *et al.* 1999). These anomalies in California caused patchy deforestation followed by rapid recovery (Tegner & Dayton 1987; Tegner *et al.* 1997). Such physiological stresses are likely to be more common toward the low latitude limits of kelp ranges. For example, the northern limit of three species of brown algae in northern Chile shifted south toward higher latitudes following the El Niño event of 1982–1983 (Peters & Breeman 1993). Such stresses may make kelps more susceptible to disease. Low-latitude kelps in northern New Zealand have succumbed to a disease that may have resulted from physiological stress (Cole & Babcock 1996; Cole & Syms 1999).

Within mid-latitudes (roughly between 40° and 60° latitude) where kelp development is less likely to be limited by physical processes such as temperature, nutrients and light, deforestation most often results from sea urchin herbivory (Table 2; Leighton *et al.* 1966; Lawrence 1975; Duggins 1980; Himmelman 1980; Dayton 1985*a,b*; Estes & Duggins 1995; Mann 2000). This is most evident in the Northern Hemisphere where the most widespread and long-lasting herbivore-induced kelp deforestations have resulted from sea urchin grazing (Table 3). These primarily *Laminaria*-dominated kelp forests (Fig. 1) have been reduced in historical times to coralline-dominated 'urchin barrens' in the Aleutian Islands of Alaska, the Gulf of Maine, Canadian Maritimes (to Newfoundland; Himmelman 1980), northern Japan (Hokkaido Island), Iceland and northern Norway (Table 3). South of those regions, forests either remain intact, such as in southern California (Dayton *et al.* 1984), or are deforested patchily in relatively few regions, such as in southern Norway (Sivertsen 1997), Ireland (Kitching & Thain 1983), the UK (Kain 1975) and southern Japan (Honshu Island; Fujita 1998).

Kelp deforestation from sea urchins is less common in the Southern Hemisphere (Table 3). In Chile, extensive sea urchin deforestation at mid latitudes (54°–46° S) was reported by Dayton (1985*b*). However that study and others (Table 3) report only patchy deforestation in north central Chile (i.e. 32° S latitude; Ojeda & Santelices 1984). Dense *Macrocystis* forests with few urchins have been described in the southernmost regions of South America (around 55° S latitude) in Chile (Castilla & Moreno 1982; Santelices & Ojeda 1984*b*) and Argentina (Dayton 1985*b*). While south-

ernmost Chile has four sea urchin species (*Loxechinus albus*, *Pseudechinus magellanicus*, *Arbacia dufresnei* and *Austrocidaris canaliculata*), they subsist on drift kelp and rarely graze attached *Macrocystis* plants. Along the east coast of southernmost South America to the northern limit of kelps in Argentina (42° S latitude; Barrales & Lobban 1975), the sea urchin, *Arbacia dufresnei* is the dominant herbivore but its grazing impact on kelp forests is minimal (Barrales & Lobban 1975).

Elsewhere in the Southern Hemisphere, sea urchin deforestation is patchy or restricted to particular depth zones. In New Zealand, a band of sea urchin 'barrens' exists at depths of around 10 m (Choat & Schiel 1982). Urchins there may be prevented by wave turbulence from grazing shallower zones. In south Australia, kelp deforestation is restricted to regions of high spatial heterogeneity that provide shelters for nocturnally grazing sea urchins (Andrew 1993). Recent kelp deforestation in Tasmania resulted from newly established high-density sea urchin populations (C. Johnson, personal communication 2002). In South Africa, sea urchins alone do not overgraze kelp forests (Velimirov *et al.* 1977) but grazer-induced phase shifts can occur from a diversity of herbivores (G.M. Branch, personal communication 2002).

Whatever regulates sea urchin abundances or their grazing behaviour often controls the distribution and abundance of kelp forests (Tables 2 & 3). Predators are commonly strong interactors (*sensu* Paine 1980) and as such are the single most important agent controlling sea urchin populations (Cowen 1983; Duggins 1983; Tegner & Levin 1983; Estes & Duggins 1995; Sala *et al.* 1998; Steneck 1998). When sea urchin predators become the focus of intense and unsustainable fishing that extirpates them, hyperabundances of the sea urchins and kelp deforestation often result (Lawrence 1975; Estes & Duggins 1995; Steneck 1998). Exceptions to this pattern are found at lower latitudes, where diverse guilds of kelp forest herbivores and predators compensate for the loss of a single predator species. Sea urchin abundance can also be influenced by other factors such as disease (Table 2; Fujita 1998; Scheibling *et al.* 1999), turbulence (Choat & Schiel 1982) and storms (Dayton 1985*a*; Ebeling *et al.* 1985) that can locally or periodically reduce sea urchin abundance and thus control kelp forest development indirectly (Foster & Schiel 1985).

Widespread, long-lasting kelp deforestation from sea urchins may be a relatively recent phenomenon. In the Aleutians of Alaska, the transition may have occurred early in the 20th century (Estes & Duggins 1995). In Japan, fisherfolk observed deforestation and patches of corallines first in the early 1930s (Fujita 1987; 1998), although sea urchins were not mentioned at that time. Later, growing sea-urchin-grazed coralline patches were reported during the 1950s to 1960s (Ohmi 1951; Fujita 1998). In California during the 1960s, the term 'barrens' was coined to describe sea urchin-induced kelp deforestation (Leighton *et al.* 1966). In the North Atlantic, the first gaps in kelp forests were reported in the 1960s for the Gulf of Maine (Lamb & Zimmerman 1964), Nova Scotia (Edelstein *et al.* 1969; Breen & Mann 1976),

Table 2 Present impacts on kelp forest ecosystems scored along a continuum: non-existent (blank), minimal (1), modest (2), great, but local (3), both great and widespread (4). The sign of the impact index number reflects whether impact tends to reduce kelp forests (–) or cause them to increase (+). No sign indicates the impact can be positive or negative (for example, nutrient cycles).

<i>Potential impacts</i>	<i>Direct human impacts</i>	<i>North-west Atlantic impacts</i>	<i>Aleutians, Alaska impacts</i>	<i>Southern California impact</i>
<i>Direct kelp harvest</i>	Yes			–1 (Dayton <i>et al.</i> 1998)
<i>Herbivory: sea urchin grazing</i>		–4 (Steneck 1997)	–4 (Estes & Duggins 1995)	–3 (Leighton <i>et al.</i> 1966)
Fishing on sea urchins	Yes	+4, Maine, USA (Steneck 1997)		+1 (Tegner & Dayton 1991)
Disease		+4, Nova Scotia, Canada (Scheibling 1986; Steneck 1997; Scheibling <i>et al.</i> 1999; Levin <i>et al.</i> 2003)	+2 (Pearse & Hines 1979)	
Storms				+2 (Harris <i>et al.</i> 1984; Harrold & Reed 1985)
<i>Herbivory: other grazers</i>		–2, Lacuna snails (Johnson & Mann 1986)	–1, Steller's sea cow (Domning 1972)	–1, Steller's sea cow, abalone (Tegner & Levin 1983; Dayton <i>et al.</i> 1999)
<i>Predation on sea urchins</i>				
Reduced (fishing pressure)	Yes	–4, cod (Steneck 1997)	–4, sea otter (Estes & Duggins 1995; Dayton <i>et al.</i> 1998)	–3, sheephead fish (Cowen 1983; Dayton <i>et al.</i> 1998)
Increased (predator switching)		+2, crabs (Tegner & Levin 1983)	+3, killer whales (Estes <i>et al.</i> 1998)	
<i>Competition from non-native species</i>	Yes			
Epiphytes	Yes	–2, bryzoan (Scheibling 1986; Scheibling <i>et al.</i> 1999; Levin <i>et al.</i> 2003)		
Exploitative competition	Yes	–2, <i>Codium</i> sp. (Lambert <i>et al.</i> 1992; Steneck & Carlton 2001)		–1, <i>Sargassum</i> sp. (Dayton <i>et al.</i> 1998)
<i>Pollution</i>	Yes			
Eutrophication	Yes			–1 (Tegner <i>et al.</i> 1995)
Sedimentation	Yes			–1 (Tegner <i>et al.</i> 1995)
Oil spills	Yes		–1 (Dean & Jewett 2001)	–1 (Dayton & Tegner 1990)
<i>Climate change</i>				
El Niño				–3 (Tegner & Dayton 1987, 1991; Dayton <i>et al.</i> 1998)
La Niña				+2 (Dayton <i>et al.</i> 1998)
Global warming	Yes	1		–1 (Dayton <i>et al.</i> 1998)
Storm frequency and intensity		–3 (Witman 1987)	–2 (Ebeling <i>et al.</i> 1985; Tegner <i>et al.</i> 1996a)	–3 (Pearse & Hines 1979; Ebeling <i>et al.</i> 1985; Tegner <i>et al.</i> 1996a; Dayton <i>et al.</i> 1998)
<i>Season cycles</i>				
Nutrient availability		1 (Chapman & Craigie 1977; Gerard 1997)		2 (Gerard 1982; Zimmerman & Kremer 1984, 1986)

Ireland (Ebling *et al.* 1966), and the UK (Jones & Kain 1967). Gaps in kelp forests in the western North Atlantic coalesced and expanded during the 1970s and 1980s in Nova Scotia (Mann 1977) and the Gulf of Maine (Steneck 1997).

Expansive coralline 'barrens' existed in Newfoundland in the late 1960s (Himmelman 1980) and possibly were present there earlier (Hooper 1980). In the eastern North Atlantic, widespread urchin-induced deforestation was first observed

Table 3 Comparison of subtidal kelp forest ecosystems of the world. Numbers in parentheses denote number of ecologically important species in subtidal kelp forests for specified taxa.

Site and latitude	Kelps and their controlling agents				Spatial and temporal scale of deforestation				
	Dominant kelps	Deforesting herbivores	Predators or diseases of kelp herbivores	Drift kelp, disease, oceanography	Regional distribution	Depth range	Local distribution	Duration deforested	References
<i>Western North Atlantic</i>									
Nova Scotia 43–45° N	<i>Laminaria</i> (1), <i>Agarum</i> (1)	Echinoid (1)	Fishes (2), urchin disease	Drift, disease	Widespread	Broad	Homogenous	Decades	Tables 1, 2, 4; Fig. 5
Maine 43–44° N	<i>Laminaria</i> (1), <i>Agarum</i> (1)	Echinoid (1)	Fishes (2) (crabs)		Widespread	Broad	Homogenous	>Decades	Tables 1, 2, 4; Fig. 4
<i>Eastern North Atlantic</i>									
North Iceland 65° N	<i>Laminaria</i> (1)	Echinoid (1)	?		Widespread	Broad	Homogenous	?	Hjorleifsson <i>et al.</i> (1995); W. H. Adey personal communication on (2001)
North Norway 65–71° N	<i>Laminaria</i> (1)	Echinoid (2)	Seabirds		Widespread	Broad	Homogenous	Decades	Hagen (1983); Bustnes <i>et al.</i> (1995); Sivertsen (1997)
South Norway 55–64° N	<i>Laminaria</i> (1)	Echinoid (1)	?		Restricted	Broad	Patchy	Decades	Sivertsen (1997)
Britain and Ireland 52–55° N	<i>Laminaria</i> (3)	Echinoids (2)	Crabs		Restricted	Broad	Patchy		Kitching & Ebling (1961); Ebling <i>et al.</i> (1966); Kain (1975)
<i>East North Pacific</i>									
Alaska (Aleutians) 50–55° N	<i>Alaria</i> (1), <i>Laminaria</i> (3), <i>Thalassiphyllum</i> (1), <i>Agarum</i> (1)	Echinoid (1)	Sea otter		Widespread	Broad	Homogenous	>Decades	Tables 1, 2, 4; Fig. 3
Southern California 30–35° N	<i>Macrocystis</i> (1), <i>Laminaria</i> (1), <i>Pterygophora</i> (1)	Echinoids (3), gastropods (8), fishes (2)	Sea otter (1), fish (1), lobster (1)	Drift, Oceanographic (ENSO) events	Restricted	Broad	Patchy	<Decade	Tables 1, 2, 4; Figs. 6, 7
<i>West North Pacific</i>									
North Japan (SW Hokkaido) 39–46° N	<i>Laminaria</i> (2)	Echinoid (1–3)	Crabs, urchin disease	Oceanographic event	Widespread	Broad	Homogenous	Decades	Fujita (1998); D. Fujita, personal communication (2002)
South Japan (West Honshu) 36–38° N	<i>Undaria</i> (1), <i>Eisenia</i> (1), <i>Ecklonia</i> (1)	Echinoid (3), fish (1)	?	Oceanographic event	Restricted	Broad	Patchy	?	Fujita (1998); D. Fujita, personal communication (2002)
<i>East South Pacific</i>									
North Chile 18–42° S	<i>Lessonia</i> (1), <i>Macrocystis</i> (1)	Echinoids (2), fishes (1), gastropods (2)	Asteroids (3), fishes (3)	Drift	Widespread	Shallow	Patchy	Decades	Ojeda & Santilices (1984); Vasquez (1993); Vasquez & Buschmann (1997)
South Chile 46–54° S	<i>Macrocystis</i> (1), <i>Lessonia</i> (2)	Echinoids (1), gastropods (1)	Asteroids (1)	Drift	Restricted	Shallow	Homogenous	Decades	Dayton (1985 <i>b</i>)
Southernmost Chile 55° S	<i>Macrocystis</i> (1) <i>Lessonia</i> (2)	Echinoids (4)	Asteroids (1)	Drift	None				Castilla & Moreno (1982); Santelices & Ojeda (1984 <i>b</i>); Vasquez <i>et al.</i> (1984)
Argentina 42–55° S	<i>Macrocystis</i> (1), <i>Lessonia</i> (1)	Echinoid (1)	?	?	None				Barrales & Lobban (1975)

Table 3 Continued

Site and latitude	Kelps and their controlling agents				Spatial and temporal scale of deforestation				
	Dominant kelps	Deforesting herbivores	Predators or diseases of kelp herbivores	Drift kelp, disease, oceanography	Regional distribution	Depth range	Local distribution	Duration deforested	References
<i>West South Pacific</i>									
Australia (New South Wales) ~32°–35° S	<i>Ecklonia</i> (1)	Echinoids (1), fishes (1)	Fishes (2)		Widespread	Moderately deep	Patchy	?	Andrew (1993, 1994); Andrew & Underwood (1993); Andrew & O'Neill (2000)
Australia (Tasmania) ~43° S	<i>Macrocystis</i> (1), <i>Ecklonia</i> (1)	Echinoid (1)	Fish (1), lobster (1)		Restricted	Broad	Homogenous	Years	C. Johnson, personal communication (2002)
New Zealand (North Island) 34°–37° S	<i>Ecklonia</i> (1), <i>Lessonia</i> (1)	Echinoids (2), gastropods (2)	Fishes (?), lobster (1)	Kelp disease	Widespread	Mid-depth	Homogenous	Decade	Andrew & Choat (1982); Choat & Schiel (1982); Choat & Ayling (1987); Schiel (1990); Cole & Babcock (1996); Babcock <i>et al.</i> (1999); Cole & Syms (1999)
New Zealand (South Island) 41°–47° S	<i>Ecklonia</i> (1), <i>Lessonia</i> (1), <i>Macrocystis</i> (1)	Echinoids (1)	?		Restricted	Broad	Patchy	?	Schiel 1990; Schiel <i>et al.</i> (1995)
<i>East South Atlantic</i>									
South Africa ~30°–35° S	<i>Ecklonia</i> (1), <i>Laminaria</i> (1), <i>Macrocystis</i> (1)	Echinoids (1), gastropods (1)	Lobster (1), fish (?)		Widespread	Deep only	Patchy	?	Anderson <i>et al.</i> (1997); G. Branch, personal communication (2001)
<i>East Indian Ocean</i>									
Western Australia 28° S	<i>Ecklonia</i> (1)	Oceanography (high temperature and low nutrients)							Hatcher <i>et al.</i> (1987)

in northern Norway in the early 1980s (Hagen 1983; Sivertsen 1997) and in Iceland in the early 1990s (Hjorleifsson *et al.* 1995). By the mid-1970s, sea urchins were viewed as the major cause of kelp deforestation (Lawrence 1975) such that by the mid-1980s conferences were held to discuss (among other things) how sea urchins could be eradicated (Pringle *et al.* 1980; Bernstein & Welsford 1982). Sea urchin-induced kelp deforestation was widely reported in mid-latitudes of the Northern Hemisphere from 40°–60° N (higher in the eastern North Atlantic due to the Gulf Stream) during the 1960s and 1980s. At the time, some researchers openly wondered if kelp deforestation was an 'irreversible degradation' (Mann 1977).

LONG TERM TRENDS: THREE NORTH AMERICAN CASE STUDIES

Kelp forests live in a balance between forces contributing to their development and deforestation. The geography of both physical and biological forcing functions for kelp forest development and persistence is complex. We know that many kelp forests look and behave very differently today from their historical counterparts. Many of these differences are due, directly or indirectly to human perturbation of physical or biological components of kelp ecosystems. Some of the most impressive changes result from trophic cascades, largely through the functional elimination of apex predators. These play out over a period of decades, centuries or longer. Here we illustrate this point with long-term historical

chronologies, some known and others inferred, from Alaska, the western North Atlantic, and southern California. These three systems are among the best studied in the world and the only ones we know for which archaeological data exist.

Alaska

The kelp forest ecosystems of the eastern North Pacific likely arose during the last 20–40 million years with the evolution of kelps, stronglycentrotid sea urchins, sea otters, and the now extinct Steller's sea cow (Estes *et al.* 1989). Kelp forests probably dominated ice-free coasts throughout this region since the last glacial period (Table 4). During the Pleistocene, sea cows ranged from Japan, throughout the North Pacific to at least Monterey Bay in California (Jones 1967). They may have been extirpated from most of their range by aboriginal hunting at the end of the Pleistocene and early Holocene, because they survived thousands of years longer in the Commander Islands, a region that was not peopled until the time of European contact in 1741 (Estes *et al.* 1989). European fur traders killed the last sea cow 27 years later. The impact of sea cows on kelp forests is unknown. However they had no teeth, probably were unable to dive and thus were most likely a trophic specialist of canopy kelps (Domning 1972; Clementz 2002). Kelp canopies are remarkably resilient to cropping of their most distal fronds and currently, in California, they support a multi-million dollar industry of canopy-cropping factory ships that sustainably

harvest kelp for their valuable alginates. If harvesting factory ships do little permanent damage to kelp forests (Tegner & Dayton 2000), it is unlikely that sea cow grazing of canopies deforested kelp beds.

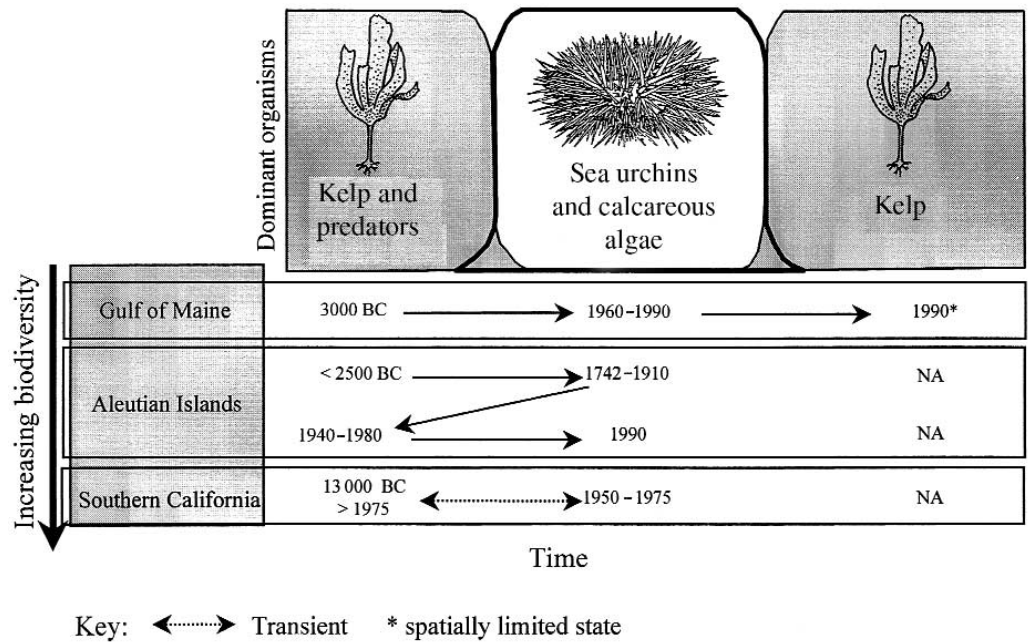
It is possible that the concentration of food associated with highly productive North Pacific kelp forests attracted early maritime people and facilitated some of the earliest migration of people from Eurasia to the Americas. It is now apparent that anatomically modern humans had colonized the Ryuku Islands south of Japan between 35 000 and 25 000 years ago and that boats were in use along the Japanese coast by about 25 000 years ago (Erlandson 2001). The readily-available shellfish, finfish, and marine birds and mammals may have allowed human populations to become established, proliferate and grow well before landward migration and the eventual development of agriculture began. Furthermore, climatic conditions along the land-sea margin were benign compared with more inland areas. It is possible that the whaling tradition of indigenous people of the North Pacific began with the overharvest of the predator-naïve and defenceless Steller's sea cow, focusing thereafter on cetaceans that were more difficult to harvest, once the sea cows were extirpated (Domning 1972). Currently, the earliest evidence for human occupation of the southern Alaskan coast (Aleutians to south-east Alaska) dates to between 9000 and 10 000 years ago, although rising post-glacial sea levels may well have submerged earlier sites.

Alaskan kelp forests are likely to have been well developed before human contact because sea otter predation on sea

Table 4 Spatial and temporal scale of change among three kelp forest ecosystems in North America.

<i>Event</i>	<i>North-west Atlantic</i>	<i>West Aleutian islands</i>	<i>Southern California</i>
Pristine state (prior to human contact)	Kelp forest	Kelp forest	Kelp forest
Scale (patch size)	100–500 km ² (Johnson & Mann 1988)	200–1000 km ² (Estes <i>et al.</i> 1989)	<10 km ² (Harrold & Reed 1985; Tegner <i>et al.</i> 1996a)
First human contact/occupation (years before present)	10 000 (Bourque 1995)	8000 (Simenstad <i>et al.</i> 1978)	12 000–13 000 (Erlandson <i>et al.</i> 1996)
Marine organisms present in diet (years before present)	5000 (Bourque 1996)	4500 (Simenstad <i>et al.</i> 1978)	11 600 (Erlandson <i>et al.</i> 1996)
First known phase change (years before present)	?–40 (Adey 1964)	2500 (Simenstad <i>et al.</i> 1978)	4000–6000 (Salls 1991, 1995; Erlandson <i>et al.</i> 1996; Erlandson & Rick 2002)
First European contact/exploitation (years before present)	460–400 (Steneck 1997)	260 (Simenstad <i>et al.</i> 1978)	460–200 (Simenstad <i>et al.</i> 1978)
Kelp bed re-establishment rate (years)	0.5–4 (Johnson & Mann 1988; Dayton <i>et al.</i> 1999)	2 (Estes <i>et al.</i> 1989)	0.5 (Harrold & Reed 1985; Tegner <i>et al.</i> 1996a)
Alternate (kelp free) state	Coralline/urchin	Coralline/urchin	Coralline/urchin
Storms remove dominant kelp	Small scale removal (Johnson & Mann 1988)	—	Large scale removal
Recent apex predators	Crabs (Leland & Steneck 2001)	Killer whales (Estes <i>et al.</i> 1998)	—
Introduced competitors	Bryozoan, <i>Codium</i> (Lambert <i>et al.</i> 1992)		

Figure 2 Timing of phase changes in community state of kelp forests of North America. Kelp with vertebrate predators, sea urchins without kelp and kelp without predators have been identified for some or all of the case study locations. Kelp forests are listed from the greatest number of trophic levels on the left to fewest trophic levels on the right. Case studies are listed from lowest species diversity in Maine to highest diversity in southern California. See text or Table 4 for references.



urchins prevented overgrazing on kelp (Simenstad *et al.* 1978; Estes *et al.* 1998; left side Fig. 2). Aboriginal Aleuts greatly diminished sea otters beginning around 2500 yr BP with a corresponding increase in the size of sea urchins (Simenstad *et al.* 1978). European and North American fur traders subsequently hunted the remaining otters to the brink of extinction in the 1700 and 1800s, causing the collapse of kelp forests as they were grazed away by sea urchins released from sea otter predation (middle of Fig. 2 and Fig. 3). Legal protection of sea otters in the 20th century reversed their decline and the resultant trophic cascade (Fig. 3), but kelp

forests have disappeared again over vast areas of the southwest Alaska coast as sea otter populations have fallen prey to killer whales (Estes *et al.* 1998). The whales apparently shifted their diet to sea otters from seals and sea lions, after the latter populations declined significantly. The pinniped declines are likely to have been caused by changes in the open ocean. Whether these changes were natural or anthropogenic remains uncertain.

Western North Atlantic

Kelps and sea urchins in the Gulf of Maine were derived from the North Pacific by way of the transarctic interchange (Durham & MacNeil 1967; Vermeij 2001). Sea otters did not make this journey. On arriving in the north-western Atlantic, however, sea urchins encountered functionally-similar predators, namely Atlantic cod and other large groundfish, which maintained the kelp-dominated state via a trophic cascade. These predatory fishes have been present in the Gulf of Maine archaeological record for at least 5000 years (Bourque 1995; Steneck 1997).

Indigenous fishers exploited cod by hook and line for thousands of years (Bourque 1995, 2001; Steneck 1997). They maintained a varied diet of marine organisms such as cod, other fish, oysters and clams, as well as terrestrial animals such as deer and sea mink, the latter now extinct (Bourque 1995). When the first Europeans explored the Gulf of Maine, the abundance of large fish impressed them (Rosier 1605). Vespucci marked the western North Atlantic coast on his 1526 map of the New World *Bacallaos*, which is Portuguese for ‘land of the codfish’. In 1602, Bartholomew Gosnold named Cape Cod for the myriad fish that ‘vexed’ his ship. By all accounts, cod and other large predatory fish were stable components of coastal zones throughout the western

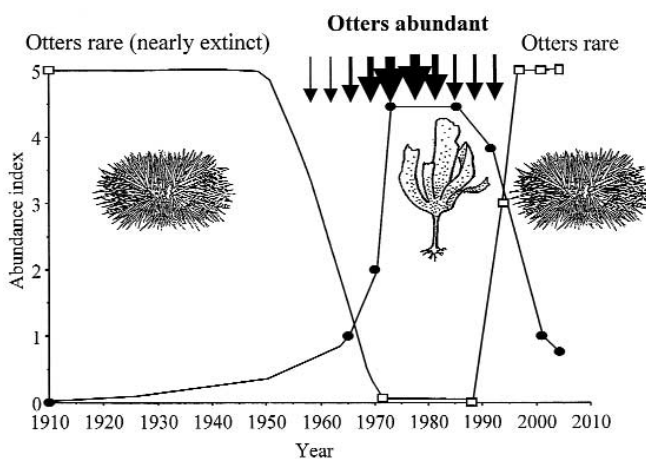


Figure 3 Temporal trends in kelp forests, predators and sea urchins of Amchitka, Alaska. Abundances estimated from several studies (see text) and Estes and Duggins (1995). Arrows indicate the timing of change in major community-changing forcing functions. Width of arrowheads indicates magnitude of the forcing function’s impact.

North Atlantic (Steneck 1997). Further, in rare offshore habitats where large predatory fishes still persist, urchins are rare, kelp is abundant (Vadas & Steneck 1988, 1995) and attack rates on tethered sea urchins are high (Vadas & Steneck 1995). Significantly, very small urchins (a few millimetres in diameter) were found at this site indicating that they can recruit but do not, probably because of high fish predation rates (Vadas & Steneck 1995).

We surmise that kelp forests dominated the benthos while predatory finfish were abundant in coastal zones through at least the 1930s. The earliest reports of algae support that supposition. Hervey (1881) described all three dominant kelp species (Table 1) as being 'very abundant from Greenland to Cape Cod' and often 'washed ashore in great numbers'. Windrows of kelp detritus are good indicators of a kelp-forested state (Novaczek & McLachlan 1986), there was no mention of expansive patches of coralline algae at that time and the earliest scientific study in the region (Johnson & Skutch 1928) reported that kelps were the 'most characteristic plant in the midlevels of the sublittoral zone.' Similarly, Nova Scotia was described as kelp-dominated in the early 1950s (MacFarlane 1952).

Extensive fishing grounds for cod and other predatory fishes were first mapped for coastal zones in Maine in the 1880s and then again in the 1920s, with remarkably little change in areal extent or location (Steneck 1997). Cod stocks persisted until mechanized fishing technology and on-board refrigeration allowed spawning aggregations of cod to be targeted in the 1930s (Rich 1929; Conkling & Ames 1996). This set off a rapid decline in the numbers and body size of coastal cod in the Gulf of Maine (Steneck 1997; Jackson *et al.* 2001). Data from 5000 year old Indian middens, and from fisheries over the past century document a relatively recent but rapid decline in the average cod body-size, coincident with their extirpations from coastal zones (Jackson *et al.* 2001; Steneck & Carlton 2001). Dominant fish predators in the coastal zone were replaced by small, commercially less important species such as sculpins (Steneck 1997). Today, large predatory finfishes remain functionally absent from coastal regions of the western North Atlantic (Steneck 1997).

Predatory fishes consume and control the distribution and abundance of sea urchins (Keats *et al.* 1986; Vadas & Steneck 1995). The extirpation of coastal cod and other fishes by the 1940s in the Gulf of Maine resulted in functional loss of apex predators, which fundamentally altered coastal food webs as lobsters, crabs and sea urchins all increased in abundance (Steneck 1997). In the 1960s, scuba diving allowed coastal ecosystems to be observed and described *in situ* for the first time. The coastal Gulf of Maine was described then as a mosaic of kelp forests (Lamb & Zimmerman 1964) and widely spaced 'barren' patches of sea urchins and coralline algae (Adey 1964; W.H. Adey, personal communication 2001; Fig. 4). Similar patches were described a decade later in Nova Scotia (Breen & Mann 1976; Fig. 5). Over the next two decades, sea urchin abundances increased throughout the Gulf of Maine, kelp forests declined and coralline barrens

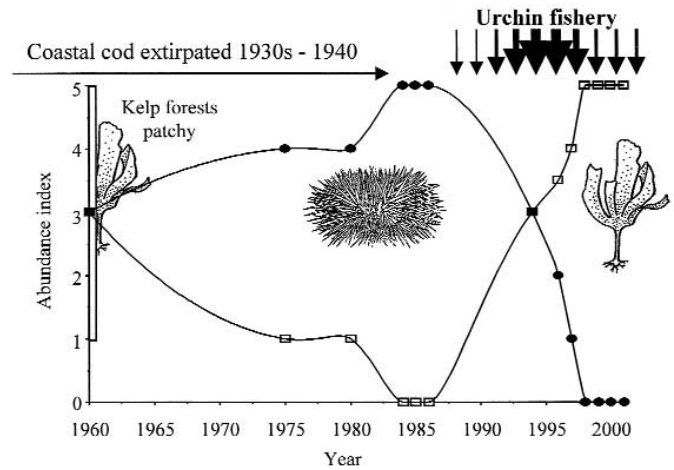


Figure 4 Temporal trends in kelp forests and sea urchins in the Gulf of Maine in the western North Atlantic. Width of arrowheads indicates the magnitude of the forcing function's impact.

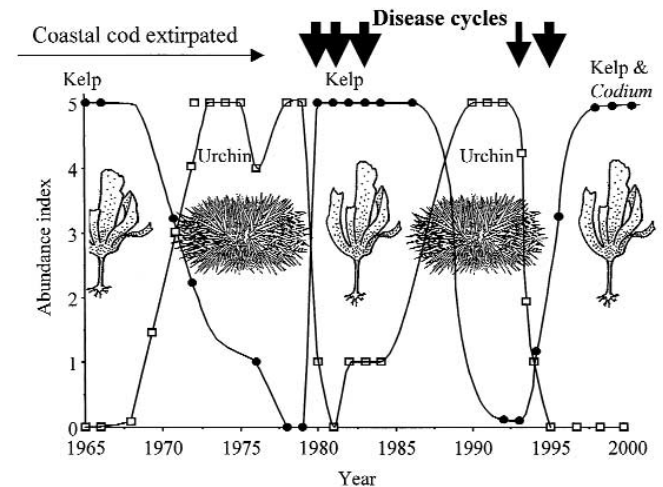


Figure 5 Temporal trends in kelp forests and sea urchins of Nova Scotia. Abundances estimated from Edelstein *et al.* (1969), Breen and Mann (1976), Warton and Mann (1981), Scheibling and Stephenson (1984), Scheibling (1986) and Johnson and Mann (1988). Width of arrowheads indicates the magnitude of the forcing function's impact.

grew and coalesced (Steneck 1997; Fig. 2). From the mid 1980s to the early 1990s, kelp forests reached an all-time low in their distribution and abundance throughout the region (Steneck 1997). Similar developments were observed in Nova Scotia, except that the system there was punctuated with disease-induced mass mortality of urchins causing it to rapidly oscillate between forested and deforested states (Fig. 6, discussed below). Arguably, the conditions for high densities of sea urchins that repeatedly denuded coastal zones of eastern Nova Scotia were only possible after the system became functionally free of apex-predators (middle and right sides of Fig. 2).

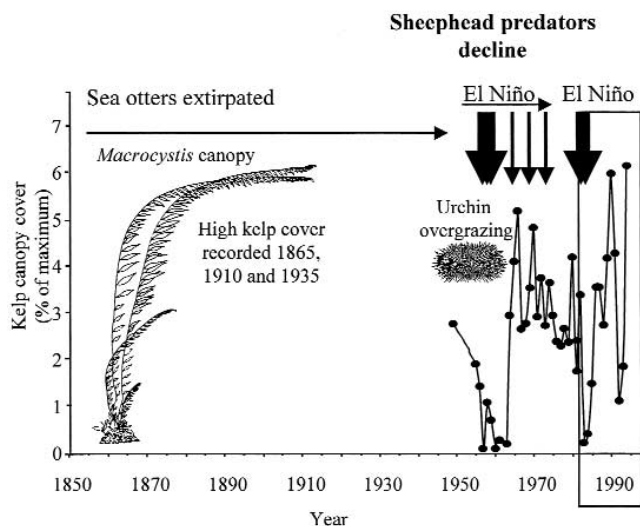


Figure 6 Temporal trends in kelp forests of Point Loma California. Abundance estimates summarized in Leighton *et al.* (1966), Tegner *et al.* (1996a), McGowan *et al.* (1998) and Tegner and Dayton (2000). Width of arrowheads indicates the magnitude of the forcing function's impact. The boxed area on the right of the figure indicates a period of high resolution subtidal data (see Fig. 3).

In 1987, a fishing industry developed to harvest Maine's sea urchins for their highly valued roe. This caused a remarkably rapid decline in urchin distribution and abundance (Steneck 1997; Vavrinc 2003). In response, kelp forests recovered, but were now without a functional herbivore trophic level (right side of Fig. 2). As a result, primary production was enhanced, and the revegetated habitat also increased the recruitment potential for some fish (Levin 1991, 1994) and crabs (McNaught 1999). Newly-settled crabs (*Cancer* spp.) survived in high numbers and became micro-predators of settling sea urchins. The micro-predator impact of crabs on urchins is striking because they can consume entire cohorts of settling sea urchins over large areas. Areas with rates of urchin settlement exceeding 10 000 individuals m^{-2} had no survivors a year later due to crab micro-predation (McNaught 1999). The phase change to macroalgae in the absence of large predatory finfish allowed large populations of adult-sized crabs to accumulate. Experiments to reintroduce adult sea urchins to population densities historically maintained prior to the sea urchin fishery resulted in attacks by swarms of large crabs (Leland 2002). In 2000, all 24 000 introduced urchins were consumed within two months. Similar patterns were observed in 2001 on a second attempt to reintroduce adult urchins to the region (Leland 2002). Thus a new 'apex' predator has emerged in coastal zones of the Gulf of Maine with functionally the same impact of vertebrate apex predators. Fished-down coastal food webs in the western North Atlantic resulted in an herbivore-free alternate stable state dominated for the time being by kelp.

California

The highly diverse food web of southern California kelp forests historically included several herbivorous species of sea urchins, small crustaceans, abalone and other snails as well as their predators including sea otters, spiny lobsters and large sheephead labrid fish (Table 1). At the time of early European contacts (AD 1542–1769), the kelp-laden and protected coastlines of the southern California Bight supported one of the highest concentrations of hunter-gatherers in human history. Archaeological evidence shows that maritime Indians colonized California's northern Channel Islands at least 12 000–13 000 years ago (Erlandson *et al.* 1996; left side of Fig. 2; Table 4). These early maritime people had seaworthy boats and by 10 000 years ago developed the first hook and line fishery in the Americas (Rick *et al.* 2001). They relied heavily on marine resources associated with kelp forests such as abalone shellfish, sheephead and marine mammals (Erlandson *et al.* 1996). Human settlement proliferated through the Holocene and later Indian peoples may have exploited kelp forest predators and herbivores with sufficient intensity to cause localized phase-shifts. In San Clemente Island middens, the size of sheephead bones decreased as prehistoric human populations increased with increased fishing intensity and a later overlying stratum was composed almost entirely of purple sea urchin remains (Salls 1991, 1995). Similar urchin 'lenses' have been noted at several San Miguel Island sites, all of which, so far, date to the last 3500–4500 years. This suggests that Indians may have created local sea-urchin barrens by hunting such sea urchin predators as sea otters and sheephead (Erlandson *et al.* 1996). If these were the first human-induced phase shifts in the system, they occurred thousands of years after first human contact and appear to have been localized and short-duration events (Table 4). After European contact, traditional fishing economies of Native American peoples were severely disrupted and effectively ended as their populations were decimated by old-world disease epidemics and colonial oppression (Tegner & Dayton 2000; Erlandson & Rick 2002).

The maritime fur trade functionally eliminated sea otters from southern California by the early 1800s (Tegner & Dayton 2000). However, widespread phase shifts to the deforested state were not observed until 150 years later (Tegner *et al.* 1996a; Fig. 6). This apparent lag timing between local sea otter extinction and urchin-induced phase shifts in kelp forest probably resulted from the buffering influences of alternate predators, herbivores and competitors (Table 1; Cowen 1983; Tegner & Levin 1983; Schmitt 1987). Spiny lobsters and sheephead are both subtropical generalist predators that feed on sea urchins and reach their northern range limits in southern California (Dayton *et al.* 1998; Tegner & Dayton 2000). Sheephead became larger and more abundant after Native Americans stopped fishing on them. It is also possible that their populations along with that of spiny lobsters increased in abundance following the sea otter's

demise. Several species of abalone (*Haliotis* spp.; Table 1) share food and habitat with sea urchins and these competitors may also have kept urchin populations in check (Tegner & Levin 1983). Released from predation by otters and Native Americans, populations of several abalone species expanded and became targets of a new fishery beginning in 1850 (Cox 1962; Tegner & Dayton 2000).

During the mid-20th century, intensified fishing pressure on the remaining predators (spiny lobster and sheephead) and herbivorous competitors (five species of abalones) may have relaxed the predation and competition that had been controlling sea urchin populations and phase shifts became widespread for a relatively brief period of time (Fig. 4). Spiny lobster landings peaked in 1894, and then stabilized at lower levels. However, the larger lobsters, those most adept at killing adult sea urchins (Tegner & Levin 1983), had become rare. Fishing pressure on large male sheephead increased after the advent of skin diving in the 1940s and accelerated in the 1950s with the loss of alternative targets (Dayton *et al.* 1998). Abalone harvests accelerated in the 1950s, causing widespread population declines by the late 1960s such that these grazers are also now functionally extinct. El Niño events, pollution discharge and sedimentation accelerated the loss of kelp, which, along with an increase in destructive urchin grazing, resulted in a phase shift to a largely kelp-free state in the 1950s and 1960s (Fig. 6). Finally, a sea urchin fishery developed and expanded rapidly in the early 1970s, reducing grazing pressure in some areas (Tegner & Dayton 1991). Commercial harvesting reduced the distribution, abundance, and body size of exploited urchin stocks, leading toward another phase shift back to a forested state. In 1988, a market developed for live sheephead, which resulted in their virtual elimination as a predator in this system (Tegner & Dayton 2000). Thus the diversity of functionally important species in southern California continues to decline, and, in time this could make the system as a whole less resistant to phase shifts. The few breaks in the canopy kelp that occurred since 1965 resulted from strong storms related to El Niño or La Niña events (Fig. 6) or occasional outbreaks of small herbivorous crustaceans released from their predators due to El Niño southern oscillation (ENSO) changes in coastal oceanography. Intense storms in 1983 and 1988 reduced the density of the three dominant kelp genera (*Macrocystis*, *Pterygophora* and *Laminaria*; Fig. 7), but recovery was rapid due to high recruitment into the breaks in the *Macrocystis* canopy (Tegner *et al.* 1997). In general, the greater diversity of southern California kelp forests, including urchin predators no longer harvested by Native Americans after Spanish colonization, may have buffered the phase shift to a deforested state and facilitated recovery from physical (oceanographic) disturbances. However, this system has experienced serial trophic-level dysfunction, beginning with sea otters and more recently including virtually all other functionally-important predators and herbivores.

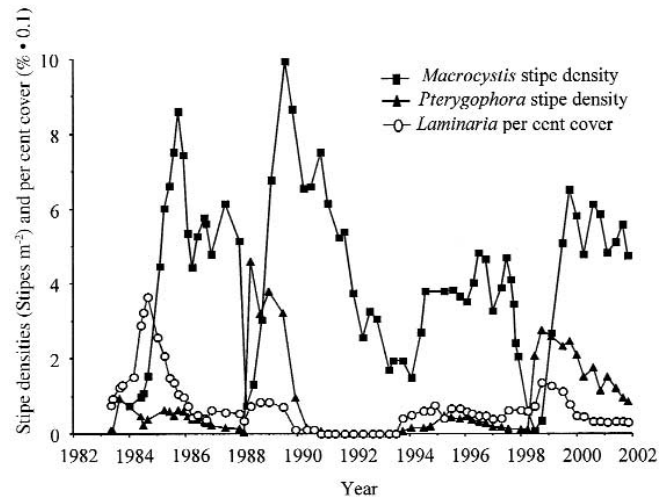


Figure 7 Temporal trends in the kelp forest of Point Loma, California, USA, 1983–1996 at 12 m depth (from Tegner *et al.* 1996a). Population density data are shown for canopy (*Macrocystis*) and stipitate (*Pterygophora*) kelps. Percentage cover data are shown for the prostrate kelp *Laminaria*.

Biodiversity, trophic cascades and rates and consequences of kelp deforestation

In the North American case studies, the extirpation of predators led to increased herbivory by sea urchins resulting in kelp deforestation at local to widespread spatial scales (Fig. 2). In the western North Atlantic and Alaska, where predator diversity is low (Table 1), the transition between kelp forests and coralline communities was rapid, frequent (Fig. 5), widespread and in some cases long-lasting (Table 4). These patterns differ from southern California, where the diversities of predators, herbivores and kelps are high (Table 1), deforestation events have been rare or patchy in space and short in duration (Harrold & Reed 1985), and no single dominant sea urchin predator exists (Fig. 6; Tegner & Dayton 2000). The biodiversity within functional nodes, such as trophic levels, is critical to the structure and functioning of kelp forest ecosystems. Nevertheless, even the most diverse systems can and are losing their functional diversity as overfishing reduces the ecologically effective population densities of important species rendering them ecologically-extinct (Estes *et al.* 1989). All of this suggests that the fragility and rate of change in kelp forest ecosystems may depend on local biodiversity. It remains an open question whether diverse kelp forests will persist or if serial disassembly and instability will inevitably result.

The consequences of kelp deforestation can affect surrounding marine and terrestrial habitats. Drift from giant kelp (*Macrocystis pyrifera*) dominates nearshore-produced phytodetritus in the Southern California bight, contributing between 60 and 99% of beach-cast autotrophic detritus (Zobell 1971). Similar estimates were made for areas adjacent

to kelp forests of eastern Nova Scotia (Mann 2000). Offshore contributions are facilitated by gas-filled floats and stipes which, when adult sporophytes are detached from the bottom due to grazing or physical disturbance, provide for long-distance dispersal by rafting (Harrold & Lisin 1989; Hobday 2000). When floating kelp rafts are deposited on the shore, the floats break, and they wash into shallow nearshore habitats and ultimately into offshore basins (Graham *et al.* 2003). Secondary productivity of both shallow (Vetter 1995) and deep-sea (Harrold *et al.* 1998) soft-sediment systems is consequently driven in a large part by allochthonous food subsidies from regional kelp resources. Kelp detritus can also make its way into nearby intertidal food webs through either the capture of fine kelp particles by filter feeders (for example, mussels [Duggins *et al.* 1989] or clams [Soares *et al.* 1997]) or large pieces of drift kelp by limpets (Bustamante *et al.* 1995; Bustamante & Branch 1996) and sea urchins (Day & Branch 2002). Kelp detritus enhances the inherently low productivity of terrestrial ecosystems on arid islands (Polis & Hurd 1996). During dry years, carbon and nitrogen from marine bird and mammal faeces and beach cast marine detritus fuel terrestrial productivity, with the greatest impact on islands with large ratios of shoreline to area (Graham *et al.* 2003). The importance of marine subsidies lessens during rainy years when high precipitation increases terrestrial production. Excellent examples are found in southern California where numerous islands of low productivity (for example, the Channel Islands) are embedded within a highly productive marine system. In addition to localized areas of high accumulation of guano and pinniped excrement, the shoreline is loaded with large quantities of kelp detritus (Graham *et al.* 2003).

POTENTIAL STATES IN 2025

Extrapolation of known trends

It is likely that climate change, human population growth, coastal development, oil spills, fisheries-induced impacts, and invasions of non-native species, will continue and possibly accelerate over the 2025 time horizon. All of these may well contribute to the continuing disassembly of kelp forest ecosystems. It is difficult to extrapolate known trends into the future, because non-linear thresholds and complex interactions can cause ecosystems to behave unpredictably (see Scheffer *et al.* 2001). Some activities may change the nature of functional relationships. For example, overfishing of predators of sea urchins can cause kelp forests to decline, but overfishing of sea urchins themselves can have the reverse effect (discussed above). Since the primary market for sea urchin roe is Japan, the currency value of the Yen could regulate fishing pressure on this driver of many kelp forest ecosystems. However it is impossible to predict how global economic markets will evolve over the next several decades.

While global temperature is expected to increase over the period to 2025, related patterns of droughts, fires, heat waves,

storms and precipitation are expected to increase in some areas but decline in others (Houghton *et al.* 1996). This underscores the limitations of attempting to generalize about kelp forest ecosystems globally. However, by considering the future of the three case studies described above, we may gain insight into some of the potential risks that befall these ecosystems with widely varying diversities and scales in space and time. Our review considers trends from the largest spatial and temporal scales to the smallest.

Ocean-climate change: global warming, regime shifts and ENSO

Ocean temperature regulates the physiology and biogeography of marine algae (Adey & Steneck 2001). Global warming, regime shifts and ENSOs are climate-driven thermal effects that can impact kelp forest ecosystems at a wide range of intensities that operate at several temporal and spatial scales. Global warming operates at the largest temporal and spatial scales (see Fig. 8), but the projected changes over the next two decades are modest compared to ocean-basin-scale regime shifts. Regime shifts cause temperature fluctuations nearly an order of magnitude greater and persist at the temporal scale of decades (Fig. 9). Superimposed on both of those changes are ENSOs, which can cause the greatest temperature anomalies but impact coastal zones at smaller scales and over periods of only a year or two. The interaction among these three ocean climate effects is complicated because each varies differently in space and time. However, when two or more thermal anomalies coincide, the compounded perturbations to kelp forests can be staggering (Paine *et al.* 1998).

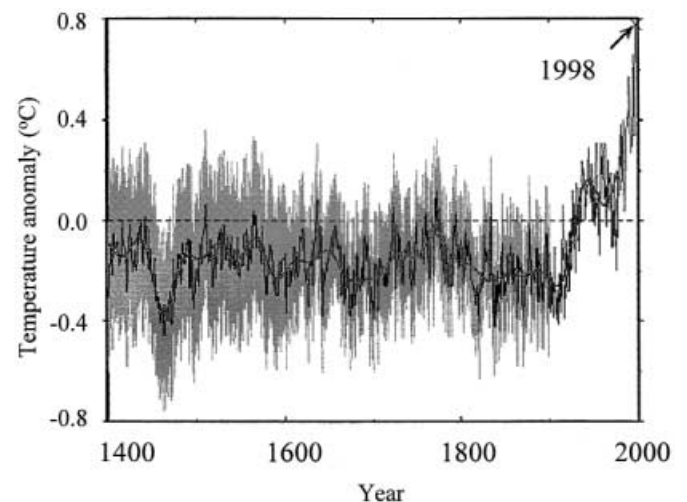


Figure 8 Temperature trends over the past 600 years in the Northern Hemisphere based on multiproxies of palaeoclimates from atmospheric and oceanographic sources (Mann *et al.* 1998). The average temperature over the 600-year period is 0.0°C. Long-term trends are evident in the average trends in 50 year running means.

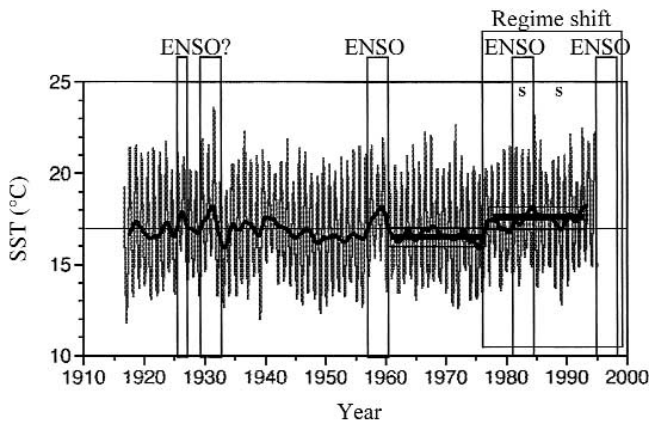


Figure 9 Recent decadal to annual thermal sea surface temperatures (SST) for southern California (from McGowan *et al.* 1998). The variable bold line over the duration of the time interval indicates the 27-month running mean. The dark horizontal lines indicate regime-shift averages of mean temperature. Superimposed boxes identify periods of regime shift and ENSOs. S = intense storms (Seymour *et al.* 1989; Dayton *et al.* 1999).

Mean annual temperature in the Northern Hemisphere has increased by 0.8°C over the past century (Mann *et al.* 1998) and is expected to increase by 0.28° – 0.58°C globally by 2025 (Houghton *et al.* 1996). The rate and magnitude of global temperature rise during the past century is unprecedented over at least the past 600 years (Fig. 8; Mann *et al.* 1998). As a group, kelps are limited to coldwater coastal zones (Fig. 1). Thus kelps living close to their upper thermal limits will be likely to recede to higher latitudes during protracted warming periods.

Temperature effects are complicated by a variety of ocean-atmosphere interactions. While the long-term frequency of strong storms in the eastern North Pacific Ocean has changed relatively little since AD 1625 (Enfield 1988), recently the frequency and intensity of extreme cyclones have increased markedly (Graham & Diaz 2001). Two storms in the 1980s were described as storms of the century (Seymour *et al.* 1989; Fig. 9). The recent steady (rather than stepwise) increase in storm activity may be related to rising sea surface temperatures in the western tropical Pacific (Graham & Diaz 2001). Thus, abiotic storm-induced disturbances of kelp forests could increase commensurate with global warming (Fig. 9). However, kelp forests usually recover rapidly from such disturbances (Tegner *et al.* 1997).

In 1982–1983, a 4 – 5°C ENSO warming halted coastal upwelling and created one of the most severe disturbances of a giant kelp forest ever documented (Paine *et al.* 1998). Nitrogen concentrations in seawater influence the welfare of kelps and vary with ocean temperature (Gerard 1997). When surface waters stratify due to ENSO or as a result of global warming, nitrogen concentrations decline and kelps become nitrogen limited and may die (Dayton *et al.* 1999). *Macrocystis* beds are particularly vulnerable because they

possess limited nitrogen storage capacity (Gerard 1982). Although nitrogen in groundwater run-off and atmospheric inputs has increased in coastal oceans (Jickells 1998), its impact is modest or undetectable relative to natural fluxes in all but enclosed basins with limited flushing (Jickells 1998). Thus, trends toward increasing temperature and decreasing nitrogen availability in kelp forests are likely to continue.

The combination of warming coastal oceans and increased stratification will be likely to shrink the geographic range of kelp beds living closest to the tropics. Indirect effects of temperature on species that influence kelp forests will be discussed below. Sea level might rise by 20 cm by the year 2050 as a result of global warming (Houghton *et al.* 1996). This could cause increased coastal erosion and turbidity, which could then affect kelp depth distribution (Vadas & Steneck 1988) and possibly other processes such as photosynthesis and recruitment (Graham 1996). Increased sedimentation could also reduce the area of substrate available for kelp settlement.

Regime shifts and ENSO events can cause thermal anomalies of shorter duration but potentially greater impact. In general, ENSO events create warmer sea temperatures along the southern California coast, but the events themselves are somewhat more frequent during regime shifts that themselves create warmer conditions on that coast (Fig. 9). Following El Niño warming comes La Niña cooling (McGowan *et al.* 1998), which is often associated with violent storms (Tegner & Dayton 1987, 1991; Seymore *et al.* 1989; Tegner *et al.* 1997).

One of the best-studied climatic regime shifts began in the mid-1970s and ended at the end of the 1990s (Steele 1998). If the new regime's duration is similar to the last two (Fig. 9), then cooler than average temperatures and perhaps lower than average ENSO and storm events may be expected over much of the next quarter century (McGowan *et al.* 1998; Fei Chai, personal communication 2002). In our case studies, only the California system was significantly affected by storms. However the duration of storm impacts is usually brief and system recovery is rapid; thus, they should have little lasting impact (Figs. 6–7; Tegner *et al.* 1997).

Changing coastal biodiversity: new apex predators and competitors

Changes in kelp forest biodiversity that affect functional components of kelp beds can disrupt the system in both predictable and unpredictable ways. The most conspicuous changes to the kelp forest result from overfishing key drivers such as apex predators and sea urchins (Estes & Duggins 1995; Jackson *et al.* 2001). Reductions in either driver can lead to trophic-level dysfunction, and alternate stable states or large-scale instabilities. For example, extirpation of sea urchin predators led to hyperabundances of sea urchins that have been stable for decades in Alaska (Fig. 3) and remarkably unstable in Nova Scotia (Fig. 5) due to epizootic disease cycles (Scheibling *et al.* 1999). Arguably, predator loss led to

hyperabundances of species setting the stage for disease-related mass mortalities (McNeill 1976).

Apex predators in pristine kelp forests were probably relatively large vertebrates. Our case studies show a consistent trend of fishing down food webs, such that large vertebrates were often targeted and extirpated relatively rapidly. Today, fish are the most commonly identified predator, but sea otters and sea ducks are also important vertebrate predators in some northern regions (Table 3). In all cases these vertebrate predators are smaller in body size and/or fewer in number than they were in the past (i.e. at first human contact). Crustaceans such as spiny lobsters and crabs are among the most important invertebrate predators (Table 3). If we extrapolate from the known trend in the Gulf of Maine case study in which extirpation of large predatory finfish led to the dominance of crabs as apex predators, then it is possible that crab predation elsewhere is the result of a disrupted trophic cascade. Crabs are dominant predators of sea urchin in Japan and in the UK (Table 3). Both of these regions have a long history of fishing that targeted and extirpated coastal groundfish. In Europe, coastal groundfish stocks were fought over in the 13th and 14th centuries and their depletion is thought to have contributed to the development of distant fisheries in Iceland and eventually North America (Kurlansky 1997). Thus it is possible that the very early extirpation of apex predators in Europe's coastal zones led to the rise of crabs as predators just as has more recently happened in the Gulf of Maine (Leland & Steneck 2001).

Overfishing in kelp forests leads to ecological (Estes *et al.* 1989) and possibly absolute (Tegner *et al.* 1996b) extinctions. This loss in biodiversity may make these systems more susceptible to invasion from non-native species (Stachowicz *et al.* 1999). Recently, kelp forests in the western North Atlantic have been invaded by the green alga *Codium fragile*, an introduced competitor that could replace the kelp species in this region, which have a long history of resilience and dominance (Fig 5; Chapman & Johnson 1990; R.E. Scheibling, personal communication 2001). The possible replacement of *Laminaria* sp. by *Codium* sp. requires sufficient breaks in the canopy for the latter species to take hold. This has been facilitated by the introduction in the 1970s of a non-native encrusting bryozoan that coats, embrittles and opens the kelp canopy every summer (Lambert *et al.* 1992; Levin *et al.* 2003). However, these two invaders join a long list of invading species that have become important players in kelp forest ecosystems of the western North Atlantic (Steneck & Carlton 2001). Species such as the common periwinkle (*Littorina littorea*) and the green and shore crabs (*Carcinus maenas*, *Hemigrapsus sanguineus*) have not only invaded, but in many cases have come to dominate the ecosystem (Steneck & Carlton 2001). Whereas other marine systems have a history of invasion, few have seen the large-scale changes in dominance evident in the western North Atlantic. The successful series of invasions there stands in stark contrast with patterns observed in the species-rich

southern California kelp forests, where introduced species generally remain subordinate to native dominants.

Declining water quality

Coastal development often reduces the permeability of soil in the watershed resulting in greater run-off and increased turbidity from plankton and particulates. If this occurred, the areal extent of kelp beds would shrink as the areal extent of the photic zone and thus their habitable area declined. Extremely low iron availability may reduce the potential productivity of kelp. If nitrogen compounds increase due to run-off, sewage disposal from population centres, or nitrogen input from atmospheric sources, nutrient availability could increase. However, human inputs of nutrients are evident only in coastal areas of restricted water exchange and most coastal zones 'appear to be still dominated by large inputs from the open ocean and there is little evidence of anthropogenic perturbations' (Jickells 1998).

In heavily urbanized areas of Japan, terrestrial deforestation and damming of rivers is thought to starve coastal zones of the iron and humic substances necessary for kelp development (Suzuki *et al.* 1995; Matsunaga *et al.* 1999). This is hypothesized to create a phase shift from kelp dominance to coralline dominance without any changes in herbivory, sea temperature or macro-nutrients (Matsunaga *et al.* 1999). We know of no other urbanized area (for example, southern California or Boston, Massachusetts, USA) where crustose coralline algae dominate shallow rocky shores without herbivore populations.

Point-source pollution is often very conspicuous, but rarely has it resulted in a serious deforestation of kelp ecosystems. A broken sewer in southern California in the late 1950s and early 1960s may have resulted in the increase of sea urchins and the decline in *Macrocystis* canopy there during that period (see Fig. 6 and previous discussion), but the impact was confounded by several other factors. The massive *Exxon Valdez* oil spill in 1989 occurred in the vicinity of kelp forests of south-west Alaska. However, kelps were minimally impacted and they recovered rapidly (Dean & Jewett 2001). For most components of the kelp forests, full recovery took two years or less (Dean & Jewett 2001). Oil covered sea otters in the spill area, and while the accounts of impacts on them are debated (Paine *et al.* 1996), the greatest impact was a decrease from around 5 otters km⁻¹ of shoreline to between 2–3 otters km⁻¹ (Paine *et al.* 1996). Otters were never absent from the system, but they may have suffered a long-term and lingering impact from oil in at least parts of spill area in Prince William Sound (Monson *et al.* 2000). While otters and other air-breathing predators may be most susceptible to oil spills, with effects similar to overfishing, that may not hold for apex predators that are fish. For example, following the *Exxon Valdez* oil spill, mortality reports estimated thousands of sea otters and sea birds died, but listed fewer than 10 dead fish from the event (Paine *et al.* 1996). Thus fish may be inherently less susceptible to oil spills, but they are by no means immune.

Given the likelihood that both non-point source and point-source pollution are likely to increase with increased human population growth, water quality is expected to continue to decline. We do not yet know if thresholds of accelerated mortality exist for declining water quality as they apparently do for increased fishing pressure. However, it is currently top-down impacts on ecosystem drivers (such as sea urchins and their predators) that most consistently denude kelp forests.

CONCLUSIONS AND MANAGEMENT

Kelps are the largest bottom-dwelling organisms to occupy the euphotic zone. Their size and photosynthesis to biomass ratio constrain their distribution globally and locally. Kelps are among the shallowest of the subtidal macrophytes. Kelp forests fail to develop at high latitudes due to light limitations and at low latitudes due to limitations in nutrients, high sea temperatures and competition from other macrophytes. In shallow mid-latitude rocky marine shores worldwide, phylogenetically diverse, structurally complex and highly productive kelp forests develop. These are uniquely capable of altering local oceanography and ecology by dampening wave surge, shading the sea floor with their canopy, providing a physical habitat for organisms above the benthic boundary-layer and by distributing trophic resources to surrounding habitats. In this context, the three kelp forest case studies from North America represent ecosystems along a continuum of natural biodiversity and human interactions. In each system we reviewed archaeological literature in an attempt to reconstruct an ecological baseline for the structure and function of kelp forests prior to contact with modern humans.

Consumer animals structure kelp forest interactions via two primary 'drivers', namely (1) herbivory by sea urchins and (2) carnivory from predators of sea urchins. Other forcing functions can be important. For example, kelps are prone to destruction and thinning by storms and competitors. Further, their growth and survival are sensitive to temperature, light and nutrient availability. However, the spatial scale and magnitude of these impacts on kelp forests are small relative to those of the consumers. Kelp deforestation worldwide results from sea urchin grazing, which is controlled by predation in kelp forests where human harvesting impacts have been minimal.

Kelp forests of the eastern Pacific may have facilitated an early coastal migration of humans into the Americas. The concentration and high productivity of vertebrates and invertebrates along this coast would have provided early human settlers with a stable source of food between 15 000 and 10 000 years ago. Archaeological data indicate that coastal settlements exploited organisms associated with kelp forests for thousands of years and this occasionally resulted in the localized loss of apex predators, outbreaks of sea urchin populations and deforestation. However, these human impacts on kelp bed systems were probably localized and relatively ephemeral.

Over the past two centuries, the commercial exploitation of kelp forest consumers led to the extirpation of sea urchin predators such as the sea otter in the North Pacific and groundfish such as Atlantic cod in the North Atlantic. In those systems, sea urchin abundances increased and kelp forests were denuded over vast stretches of coast. In the southern California system, the high diversities of predators, herbivores and kelp appear to have buffered this system from systemic deforestation.

Biodiversity of kelp forests may also help resist invasion of non-native species. In the species-depauperate western North Atlantic, introduced algal competitors carpet the benthos and threaten the dominance of kelp. Other introduced herbivores and predators have taken hold and have increased to dominate components of the system.

Global and regional climate changes have measurable impacts on kelp forest ecosystems. Increasing frequencies of ENSO events, oceanographic regime shifts and violent storms cause deforestation. This, in combination with the serial loss in biodiversity from overfishing, appears to be the greatest threat to structure and functioning of these systems over the 2025 time horizon.

Management for the conservation of kelp forest ecosystems should focus on restoring biodiversity and especially on minimizing fishing on predators. In particular, species such as sea otters, sheephead and cod should be restored to fulfil their functional role in the Alaska, California and western North Atlantic systems, respectively. While sea otters are already protected, other commercially valuable species such as Atlantic cod will be unlikely to be preserved for this ecosystem role that they perform. Ultimately, human values and political will determine the conservation agenda. Significant investment in education for stakeholders, the general public and policy makers will be necessary for this conservation goal to succeed.

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