16 GIANT KELP FORESTS, ALASKA
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CLASSIFICATION

ECOSYSTEM DESCRIPTION

Characteristic native biota
Alaskan kelp forests are structurally and functionally diverse assemblages (Figure 1). They are characterised by species of brown algae in the Order Laminariales including Nereocystis luetkeana, Laminaria groenlandica, Alaria fistulosa, Agarum fimbriatum and Thalassiophyllum sp. (Steneck et al. 2002). These create a complex and dynamic layered forest architecture up to 15 m tall, that provides substrate, shelter and foraging resource for a diverse fauna assemblage of epibenthic invertebrate herbivores (Steneck & Watling 1982) and pelagic vertebrate predators (Estes et al. 2009). Characteristic invertebrates include urchins, Strongylocentrotus franciscanus, S. purpuratus and S. droebachiensis, limpets, and starfish, Solaster spp. Fish, including the Pacific cod (Gadus macrocephalus) and rock greenling (Hexagrammos lagocephalus), are important predators that depend directly or indirectly on the ecosystem (Reisewitz et al. 2005). Characteristic mesopredators include sea otters, (Enhydra lutris), harbour seals (Phoca vitulina), Steller sea lions (Eumetopias jubatus) and northern fur seals (Callorhinus ursinus). Steller's sea cow (Hydrodamalis gigas), now extinct, was a functionally unique herbivorous member of the vertebrate assemblage (Domning 1972). Large pelagic predators are also important components of the ecosystem, including killer whales (Orcinus orca) and over 15 species of great whales including sperm (Physseter macrocephalus) and fin whales (Balaenoptera physalus).

The ecosystem is distinguished compositionally from other kelp forests, which are generally separated geographically by continental land masses or deep sea. The Alaskan kelp forests are continuous with those off California, which differ in their more diverse assemblage of macroalgae, including Macrocystis pyrifera.

Figure S16. 1. Alaskan kelp forest near Aleutian Islands (left. dominated by Cymathera triplicata in foreground with Alaria fistulosa in rear and right. dominated by Laminaria groenlandica. Photos by David Duggins, University of Washington (Source: Stony Brook University, http://life.bio.sunysb.edumarinebio/kelpforest.html).
Abiotic environment
Kelp forests are confined to cold, nutrient-rich, open, rocky coastal waters. A dependence upon light for photosynthesis restricts them to clear shallow water, rarely deeper than 15-40m.

Distribution
Alaskan kelp forests occur in nearshore marine environments of the western Gulf of Alaska, Aleutian Islands and eastern Bering Sea between latitudes of about 45–60°N (Figure 2).

![Google earth](image)

Figure S16. 2. Approximate distribution of Alaskan kelp forests off the coast of North America, north from about 40°N. Adapted from Raffaelli & Hawkins (1996) and, Steneck et al. (2002).

Key processes and interactions
Kelp canopies influence the near-shore marine environment and its biota by dampening waves, reducing light and providing a three-dimensional architecture within the water column. Through its influence on wave action and water movement, kelp affects coastal erosion, sedimentation, upwelling, benthic productivity and recruitment of benthic invertebrates (Duggins et al. 1990). Reduced light intensity under kelp canopies creates benthic conditions favourable for particular species (Santelices & Ojeda 1984) and affects competitive relationships among algal species (Dayton 1985). Kelp forest architecture provides shelter, breeding sites and food for pelagic and benthic organisms (Bernstein & Jung 1980; Bologna & Steneck 1993; Levin 1994; Anderson et al. 1997), while the kelp tissue itself provides substrates for epiphytic algae and sessile animals Duggins 1980; Reed & Foster 1984; Dunton & Schell 1987), as well as food for herbivores and detritivores (Linley et al. 1981; Duggins et al. 1989; Mann 2000), including some trophic specialists (Steneck & Watling 1982; Estes & Steinberg 1988). The kelp forests are part of an extensive trophic network that extends to the open ocean and terrestrial habitats (Estes et al. 2009; Figure 3).
Figure 2. Food-web relationships among selected species in the North Pacific Ocean and southern Bering Sea. The arrows represent linkages for which there are known (solid lines) or suspected (dashed lines) dynamic interactions. Black arrows represent top-down forcing and the grey arrows represent bottom-up forcing. Strong dynamic responses are known for food-web pathways that connect at least eight species (e.g. great whales → killer whales → sea otters → sea urchins → kelp → coastal fishes → gulls → bald eagles). See text for explanations.

Figure S16. 3. Trophic interactions intrinsic and extrinsic to Giant Alaskan Kelp Forests (from Estes et al. 2009).

Disturbance regimes, competition, and predation are key processes that influence kelp forest ecosystem dynamics. Competition strongly regulates recruitment and establishment, which occurs largely within canopy gaps created by population thinning or disturbance (Reed & Foster 1984; Chapman 1986). Structure Outcomes of interspecific competition depend on differential growth rates, which are regulated by water temperatures and availability of light and nutrients, and vary seasonally and between years (Steneck et al. 2002). Canopy gaps of varying size may be created by disturbances such as thermal events, salinity anomalies and storms, although gaps created by these physical disturbances tend to be relatively small and short-lived (Tegner et al. 1997; Steneck et al. 2002).

More extensive deforestation may result from biological interactions such as outbreaks of disease or herbivore populations. Kelps are more susceptible to lethal diseases when under physiological stress initiated by low nutrient availability, high salinity or high temperatures (Steneck et al. 2002). Herbivory by the extinct Steller’s sea cow may have influenced the availability of gaps, but its overall influence on kelp forest dynamics is poorly known (Tegner & Dayton 2000). Overgrazing by sea urchins causes the most widespread and long-lasting denudation of Alaskan kelp forests (Duggins 1983; Estes & Duggins 1995). While dense stands of kelp deter urchin attack, formation of gaps can initiate rapid conversion of kelp forests to urchin barrens (Estes et al. 2009). Once established on open substrate, the urchins eliminate kelp recruitment and maintain open conditions by switching their behaviour from consumers of detrital fallout within forest to mobile herbivores when kelp is rare (Konar & Estes 2003). The system thus tends to exhibit non-linear dynamics between well developed kelp forest and urchin barrens, with unstable transitory intermediate states, depending on otter abundance (Estes & Duggins 1995; Steneck et al. 2002; Estes et al. 2010; Figures 4 & 5). Since kelp canopies provide habitat for predatory fish and mammals, large reductions in structural complexity of the forest can increase survival of resident prey and their larvae (Gaines & Roughgarden 1987). The abundance of urchins is regulated by several trophic levels of predators and the availability of alternative prey (Figure 3), resulting in highly complex ecosystem dynamics influenced by multiple processes and interactions that are intrinsic and extrinsic to the kelp forests (Springer 2003; Springer et al. 2008; Estes et al. 2009).
Figure S16. 4. Non-linear inverse relationship between kelp density and sea urchin abundance, dependent upon presence of sea otters (from Estes & Duggins 1995, see also Estes et al. 2010).

Figure S16. 5. Urchin barren (left, photo: David Duggins. cf. kelp forest in Fig. 1, and sea otter predation on urchins (right, photo: James A. Mattison III. Source: Stony Brook University, http://life.bio.sunysb.edu/marinebio/kelpforest.html).

Threatening processes

Widespread deforestation is the major threat to Alaskan kelp forests, as this eliminates or greatly simplifies the structural complexity that provides essential habitat for characteristic native biota of the ecosystem (see previous section). Although transient kelp-free patches are likely to be expressions of natural ecosystem turnover, there is evidence that over-exploitation of marine mammals and fish can initiate a trophic cascade that results in widespread conversion of kelp forest to urchin barrens (Estes et al. 2009). As sea otters are major predators of urchins, decline in otter populations can lead to explosion of urchin populations and subsequent elimination of kelp. Otter populations are in turn regulated by predators, notably killer whales, which are thought to have switched their diet in response
to depletion of great whale and piniped populations during the second half of the twentieth century, substantially increasing predator pressure on otter populations (Springer 2003; Springer et al. 2008).

Other threats include changes to ocean currents and temperatures, as concentrations of nutrients are inversely related to water temperature, and kelp forests are dependent for growth on cold waters with high nutrient availability. For example, nitrate concentrations decline by more than an order of magnitude as temperatures increase from 6 to 14°C (Dayton et al. 1999). Thus, the kelp forests are likely to be susceptible to climate change that weakens cold water currents or increases frequency of thermal events. Oil spills also pose threats of long-lasting impacts over localised parts of the ecosystem distribution (Peterson et al. 2003).

Ecosystem collapse

For assessment of criteria A and B, the kelp forests are assumed to collapse when their distribution declines to zero and they are entirely replaced by urchin barrens. are found, with kelp density of zero, throughout the former range. Two variables were identified as potentially suitable for assessing disruption to biotic processes and interactions under criterion D: the density of kelp; and the abundance of sea otters, both having important trophic roles within the ecosystem. It was assumed that ecosystem collapse occurs when either of these measures declines to zero.

ASSESSMENT

Summary

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Criterion A

Although there is qualitative information to suggest that a substantial area of kelp forest to urchin barrens was converted to urchin barrens within the past 50 years, spatially explicit data for the recent and historic past were unavailable for this assessment. Similarly, no future projections were available for assessment. Consequently, the status of the ecosystem is Data Deficient under criteria A1, A2 and A3.

Criterion B

**Extent of occurrence:** A minimum convex polygon enclosing rocky reefs suitable for development of kelp forest along the Aleutian Islands and south Alaskan coast has an area of at least 1.5 million km². Given that the distribution may extend further east and south of this core area, the extent of occurrence of the ecosystem is likely to be larger than this estimate. Although there is evidence of continuing disruption to biotic interactions (Estes et al. 2009), the status of the ecosystem under criterion B1 is Least Concern because the estimated extent of occurrence exceeds the thresholds for all threatened categories.

**Area of occurrence:** Available distribution data are of insufficient resolution to estimate the number of occupied 10 km grid cells. The status of the ecosystem is therefore Data Deficient under criteria B2.

**Number of locations:** The most serious plausible threat to Giant Alaskan Kelp Forests is deforestation by urchins. The number of locations where urchin outbreaks occur independently is uncertain. Even though depletion of otter populations is widespread throughout the distribution of the kelp forests, this may not lead to urchin outbreaks in some cases (Tegner & Dayton 2000; Estes et al. 2010). Remnant otter colonies plausibly persist at locations in between the areas where they have been extirpated.
Furthermore, different conditions and ecological responses of urchins to otter extirpation occur in different parts of the range, possibly due to differing regional patterns in urchin recruitment (Estes & Duggins 1995; Estes et al. 2010). Consequently there are likely to be more than five locations and the status of the ecosystem is likely to be Least Concern under criteria B3.

Criterion C

Environmental degradation may occur through changes to ocean currents and temperatures (affecting nutrient availability), as well as oil spills. At this time suitable data sets to support an assessment of criterion C had not been located and hence the ecosystem is assigned to Not Evaluated.

Criterion D

The most serious disruption to biotic interactions occurs through trophic cascades involving sea otters, their predators and their prey, urchins that graze on kelp. Since densities of kelp are inversely related to densities of urchins and that phase shifts between forests and urchin barrens are related to a threshold abundance of otters (Estes et al. 2010), any of these variables is potentially suitable for assessing criterion D. Other potential response variables include the abundance of great whales and pinnipeds, since these species are alternative prey for killer whales, which putatively switched their diet to sea otters when the larger mammals sequentially became scarce (Figure 3, Springer et al. 2003). Although good data are available on population changes in great whales and pinnipeds, they were not used to assess the status of kelp forests because i. data on more proximal response variables are available and ii. the causal relationship linking great whales and pinnipeds with otter abundance via killer whale predation is less certain than the link between otters, urchins and kelp (Springer et al. 2008). The assessment is therefore based on accurate, but localised surveys of kelp density and more extensive, but less precise surveys of sea otter populations.

Current decline: Repeat survey data of kelp density (Estes et al. 2010) and aerial surveys of otter populations were used to assess the severity and extent of current declines in biotic processes of the kelp forests. It was assumed that populations of otters, urchins and kelp were essentially stable prior to about 1986 based on evidence in Doroff et al. (2003).

Survey data for kelp stipe densities were available for 2-4 years between 1987 and 2000 from seven islands, based on 7-30 sites per island (Table 1 in Estes et al. 2010). It was assumed that the seven surveyed islands, scattered across the Aleutian chain, were representative of the full distribution of the ecosystem. Rates of change in kelp density were calculated for each island assuming an exponential model and varied from 29.5% decline per year to 15.4% increase per year. A weighted average across all sites, based on initial abundance indicated that kelp densities declined on average by 49.2% over 13 years between 1987 and 2000. Subsequent trends in kelp densities are uncertain, but declines are suspected to have continued beyond 2000, with later reversal at some sites. It was assumed that ecosystem collapse occurs when kelp density is close to zero across all sites, consistent with kelp replacement by urchin barrens throughout the distribution. Based on kelp densities, the relative severity of decline was therefore estimated to be approximately 50% averaged across the full extent (100%). of the distribution for the 13 years 1987-2000. Allowing for some decline prior to 1987 or after 2000 suggests that the decline in kelp density over the past 50 years was at least 50%.

Aerial survey data for sea otters were available for 55 islands in six island groups along the entire Aleutian chain (Table 1 in Doroff et al. 2003). All islands were surveyed in 1959, 1965, 1992 and 2000. It was assumed that the surveyed islands were representative of the full distribution of the ecosystem. Total otter counts were comparable in 1959 and 1965 (9507 and 9700, respectively). By 1992, there had been a net decline to 8048 sightings, although populations had increased on some islands and declined on others (Doroff et a. 2003). By 2000, otter populations had declined to low levels on all surveyed islands, with 2442 sightings recorded in total. Over the 40 year period 1959 - 2000, the otter
population declined by an estimated 74.3%. Doroff et al. (2003) suggest this may be a conservative estimate of decline since more animals may have eluded detection in the earlier surveys due to fast flight speeds. Skiff surveys at a subset of six islands produced very similar estimates of decline between 1992 and 2000 (Doroff et al. 2003). The fate of otter populations since 2000 is uncertain, although they are believed to have recovered at some sites (Estes et al. 2009). Assuming that ecosystem collapse occurs when otter populations are close to zero across all sites, produces an estimated relative severity of decline slightly larger than 75% across the full extent (100% of the distribution. An alternative estimate of decline can be obtained from estimates of the total population reported by Doroff et al. (2003). In the mid 1980s (prior to recent decline. the total population was estimated to be 55,000 - 74,000 animals. By 2000, Doroff et al. (2003. estimated there were a total of 3,924 - 13,580 animals based on extrapolation from survey. The lower and upper bounds of otter population decline are therefore 100 × (55000-13580)/55000 = 75.3% and 100 × (74000-3924)/74000 × 94.7%, respectively, somewhat larger than the estimate obtained directly from the raw survey data. The upper bound may be extreme, as Doroff et al. (2003. caution that their 2000 estimate

Evidence from trends in kelp density and sea otter sightings suggest a decline in biotic function of 50-95% relative severity across 100% of the extent of the ecosystem. The upper bound of this range may underestimate the severity of decline because i) Doroff et al. (2003) caution that their 2000 survey may have underestimated the population due to detectability issues (although it is not known whether the estimates from the 1980s suffer similar bias) and ii) the calculations assume that otter and kelp populations have not recovered since 2000 when there is qualitative evidence of some recovery. The most likely status of the ecosystem under criterion D1 is therefore Endangered, although a status of Critically Endangered is possible.

**Future decline:** No projections are currently available for any of the biotic response variables. The status of the ecosystem is therefore Data Deficient under criterion D2.

**Historic decline:** Although historical data on kelp densities are lacking, some estimates of otter populations are available over the past century. During the nineteenth century extensive overexploitation by hunters eliminated sea otters from most of their historic range within the region, leaving only a few depleted remnant populations in the central Aleutians (Doroff et al. 2003). Harvesting ceased in 1911 when the species was protected by international treaty. This lead to recovery of the central Aleutian populations apparently to pre-harvest levels by about 1950 and by the 1980s, the species had recolonnised many other islands and the total population was estimated to be 55,000 - 74,000 animals. A second decline followed, as described under 'Current decline'. Although, in the 1980s, some otter populations were thought to have reached carrying capacity, the overall population was still expected to be recovering to pre-harvest levels due to expected increases on more recently colonised islands (Doroff et al. 2003). It may therefore be reasonable to assume that the population in 1750 was comparable or slightly larger than its peak in the mid 1980s. Based on this assumption, the decline in otter populations throughout the distribution of the kelp forest was 75-95% since 1750 the status of the ecosystem is therefore Endangered (plausible range Endangered - Critically Endangered under criterion D3.

**Criterion E**

No quantitative analysis has been carried out to assess the risk of ecosystem collapse for Coastal sandstone upland swamps. The status of the ecosystem is therefore Data Deficient under criterion E.

**REFERENCES**
