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TOWARD ECOSYSTEM-BASED MANAGEMENT OF MARINE MACROALGAE—THE BULL KELP, *NEREOCYSTIS LUETKEANA*

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Abstract Ecosystem-based management is predicated on the multifaceted and interconnected nature of biological communities and of human impacts on them. Species targeted by humans for extraction can have multiple ecological functions and provide societies with a variety of services, and management practices must recognize, accommodate, and balance these diverse values. Similarly, multiple human activities can affect biological resources, and the separate and interactive effects of these activities must be understood to develop effective management plans. Species of large brown algae in the order Laminariales (kelps) are prominent members of shallow subtidal marine communities associated with temperate coastlines worldwide. They provide a diversity of ecosystem services, perhaps most notably the fuelling of primary production and detritus-based food webs and the creation of biogenic habitat that increases local species diversity and abundance. Species of kelp have also been collected for a variety of purposes throughout the history of human habitation of these coastlines. The bull kelp, *Nereocystis luetkeana*, provides a clear example of how the development of sustainable harvest policies depends critically on an understanding of the morphological, physiological, life-history, demographic, and ecological traits of a species. However, for *Nereocystis* as well as many other marine species, critical biological data are lacking. This review summarizes current knowledge of bull kelp biology, ecological functions and services, and past and ongoing management practices and concludes by recommending research directions for moving toward an ecosystem-based approach to managing this and similarly important kelps in shallow temperate rocky reef ecosystems.

Introduction

Why the interest in ecology and ecosystem-based management of Nereocystis*?*

Among the many tenets of ecosystem-based management (EBM) of marine resources, two are central to the goal of a more comprehensive approach to resource management. First, EBM recognizes that species targeted for extraction can have multiple ecological functions and provide society with a variety of ecosystem services. Management practices therefore should strive to accommodate these diverse values (Field et al. 2006, Francis et al. 2007, Marasco et al. 2007). Second, EBM recognizes that multiple and diverse human activities, from local fisheries to global climate change, affect the state and sustainability of marine resources and the ecosystems that support them, and that a thorough understanding of both the independent and interactive effects of these activities must underpin management plans for these to be effective (Leslie & McLeod 2007, Levin & Lubchenco 2008, McLeod & Leslie 2009). As management goals move from maximizing the sustainable use of marine resources along a single axis (e.g., single species-based sustainable fishery yields) to a more comprehensive balancing of *multiple* services with each other in a manner that ensures the sustainability of those services and their associated ecosystems, knowledge of the ecological functions and services of species and of how human activities influence them will be critical. Models for both EBM and strategies to move toward EBM must recognize species that provide multiple, well-characterized ecological functions and services and that are known to be influenced by a variety of human activities.

Species of large brown macroalgae of the order Laminariales, commonly referred to as kelps, are a conspicuous component of coastal rocky reef habitats in temperate oceans throughout the world. Kelps have been harvested throughout the history of human habitation of temperate coastlines for a variety of purposes, including human consumption, the production of pharmaceuticals, and as food for commercial mariculture. However, kelps also provide a diversity of ecosystem services to the biological communities of which they are part. As such, the consequences of human impacts on kelps are not limited to the direct effects on kelp populations themselves, but also influence indirectly the many species that depend on or benefit from the presence of these macroalgae in nearshore habitats.

Along the western coast of North America, two genera, the giant kelp *Macrocystis* spp. (hereafter *Macrocystis*), and the bull kelp *Nereocystis luetkeana* (hereafter *Nereocystis*), form extensive forests in shallow (<30-m depth) rocky habitats. Because of their fast growth rate and large stature, these algae are thought to contribute markedly both to the productivity of shallow coastal marine ecosystems and as habitat for a diversity of fishes and invertebrates (Foster & Schiel 1985, Graham 2004, Graham et al. 2008). Both of these fundamental ecosystem functions of kelps are realized not only by those species that reside in kelp forests throughout their lives (i.e., kelp forest residents) but also by species that use these habitats as foraging grounds (e.g., shorebirds, sea otters) and nurseries (particularly fishes) because of the enhanced growth and survival provided to them by the productivity and structural refuge created by kelp (see review by Carr & Syms 2006). Many of the species that utilize kelp habitat have been strongly affected by overfishing and are themselves the focus of conservation efforts (e.g., abalone, rockfishes, sea otters). In addition to these effects on primary and secondary productivity in nearshore habitats, the physical barrier created by kelp forests along the shoreline dampens ocean waves, thereby reducing coastal erosion (Lovas & Torum 2001, Ronnback et al. 2007). Kelps also represent important biological links between marine ecosystems. The biomass and nutrients they produce, in the forms of detritus or entire detached plants, are exported by storms to sandy beaches and submarine canyons, where they fuel food webs in the absence of other sources of primary production (Kim 1992, Vetter 1995, Harrold et al. 1998). Floating kelp rafts may also serve as habitat for larval and juvenile fishes and invertebrates, effectively transporting them among spatially isolated local populations of adults (Kingsford 1992, Kokita & Omori 1998, Hobday 2000, Thiel & Gutow 2005). Furthermore, kelps are of great social, cultural, and economic importance because of the many human activities they foster (e.g., recreational fishing, scuba diving, bird watching, kayaking); tourism and recreation are included in one of the fastest-growing sectors of California's economy today (Kildow & Colgan 2005). Separately and in combination, the direct and indirect benefits that kelp forests provide can translate into socioeconomic values of extreme importance to local coastal communities.

Due to their close proximity to shore, kelp forests are subject to deleterious anthropogenic impacts that can impair the functions and services they provide. In addition to direct extraction, kelps can be exposed to coastal pollution in the form of nutrient discharge from urban and agricultural sources and thermal pollution associated with cooling water outflow from coastal power plants. Increases in turbidity and rates of sedimentation associated with all of these activities impair photosynthesis (i.e., growth and survival of adult plants) and smother reproductive stages and spores, preventing reproduction and germination. Beyond these localized and regional threats, kelp forests are vulnerable to environmental modification caused by global climate change. The existence and tremendous productivity of these forests rely on the upwelling of deep offshore nutrient-rich waters. This upwelling process is driven by coastal winds that move surface waters offshore, driving their replacement by the deeper nutrient-rich waters. As atmospheric conditions fluctuate in response to large-scale climate trends, changes in the timing, location, and intensity of coastal winds alter the distribution and magnitude of upwelling, thereby changing the environmental conditions required to sustain kelp forests. Large storms associated with El Niño are major causes of mortality and the loss of entire kelp forests (Tegner & Dayton 1987), and increases in the frequency, duration, and strength of El Niño in recent years may be a direct consequence of concurrent regional climate changes (Trenberth & Hoar 1996).

The direct and indirect impacts of kelp extraction depend very much on the species and means by which it is removed. Historically, extraction has been focused on the giant kelp *Macrocystis*, primarily by the pharmaceutical industry. Specially designed harvesting vessels were used to remove large swathes across forests from the upper 2 m of the canopy. The direct impact on the forests is considered minimal because the canopy is often replaced rapidly by the growth of fronds from the base of the plants. Moreover, the alga is perennial, and the reproductive tissues are located at the base of the plant and remain intact during and subsequent to harvesting. Thus, the algae are able to reproduce, and associated forests to persist, in the face of large-scale mechanical extraction. However, the indirect effects on the fishes and invertebrates that use the forest canopy as nursery habitat, and on the many species that require the flux of kelp blades from the canopy to the reef habitat below to fuel a detritus-based food web (akin to litter fall in terrestrial forests), have not been rigorously investigated.

The extraction of *Nereocystis* is a more recent development, fuelled by the demands of abalone mariculture and human consumption. Although relatively smaller in volume and geographic extent, the harvest of *Nereocystis* is problematic. Extraction is primarily by hand from a boat and, like giant kelp, limited to the upper 2 m of the forest canopy. However, the source of buoyancy that keeps *Nereocystis* plants upright, along with the alga's reproductive organs, is located at the top of the plant and is often removed during harvest. In the absence of this source of buoyancy and associated photosynthetic tissue, individual plants may sink to the bottom and die. Furthermore, because *Nereocystis* is an annual species, removal of the upper portion of plants prior to reproduction can potentially preclude the production of subsequent generations. The spores of *Nereocystis* are thought to move very short distances (tens of metres) on average; thus, local impairment of reproduction might eventually result in the disappearance of a forest, although local recruitment could be subsidized by input of spores from other populations delivered by either drifting reproductive sporophytes or abscised sori. In addition, the presence of dormant spores produced by previous generations of *Nereocystis* could potentially reseed local populations that have been depleted by harvesting. However, because there are few data on the dispersal potential and dormancy durations of spores, these mechanisms of local 'rescue' cannot at present be incorporated into management plans in a quantitative manner.

Approach, scope of synthesis, and products

The EBM of coastal marine resources is based, in part, on scientific understanding of the broad (i.e., ecosystemwide) consequences of human uses of the coastal environment, including resource extraction and degradation of habitats. To effectively manage these resources, a clear understanding of the potential threats and consequences of human activities to the resource and the ecosystem is essential. To contribute to this understanding, this report synthesizes the state of knowledge of (1) the ecology of *Nereocystis* and its role in coastal ecosystems, (2) the past and present human uses of and threats to this species and, by extension, the coastal ecosystem, and (3) the past and present approaches to managing this resource. This synthesis identifies gaps in current knowledge of *Nereocystis* biology and ecology and recommends priority research needs to inform management of the human activities that impinge on this species and its ecosystem functions and services. The scope of this review spans studies and management programs from Alaska to central California and includes data from both peer-reviewed scientific journals and non-peer-reviewed sources (e.g., reports produced by governmental agencies and non-governmental organizations [NGOs]).

Review and synthesis of the ecology of *Nereocystis luetkeana*

Species description and geographic distribution

Nereocystis is a conspicuous brown macroalga in nearshore environments along the Pacific Coast of North America (Figure 1). The blades of the alga (30–60 on an adult sporophyte, each up to 4 m long) are held near the surface of the water by a gas-filled, spherical pneumatocyst at the end of a long, slim stipe (~1/3 inch in diameter), attached to the substratum with a hapterous holdfast (Figure 2). Up to one-third of the upper portion of the stipe is hollow, and it is extremely elastic; when exposed to wave force it can stretch more than 38% (Koehl & Wainwright 1977). Because all of an individual's blades are at or near the water surface, the canopy provides virtually all substrata for photosynthesis and nutrient uptake, and photosynthate is subsequently translocated throughout the rest of the thallus via sieve elements in the medulla (Nicholson & Briggs 1972, Schmitz & Srivastava 1976).

Figure 1 A stand of *Nereocystis* on a shallow rocky reef off the coast of central California. Schooling surf perch (Embiotocidae) are visible at the bottom right. (Photograph courtesy of Steve Clabuesch.)

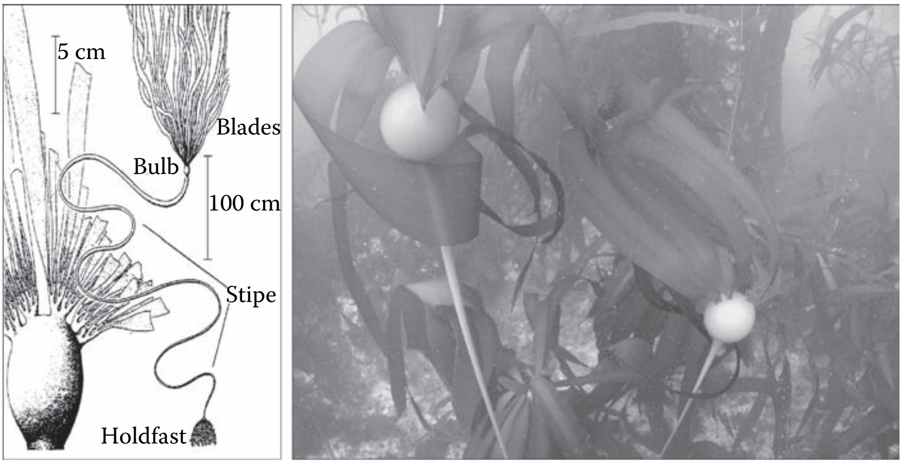

Figure 2 Morphology of *Nereocystis* plants. *Bulb* refers to the gas-filled pneumatocyst. (Diagram from G.M. Smith, *Marine Algae of the Monterey Peninsula*, copyright © 1944 by the Board of Trustees of the Leland Stanford Jr. University, renewed 1972. Photograph of young plants emerging from a sparse cover of the understory kelp *Pterygophora californica* courtesy of Steve Clabuesch.)

Nereocystis forms extensive beds from Point Conception, California, to Unimak Island, Alaska (Figure 3; Druehl 1970, Abbott & Hollenberg 1976, Miller & Estes 1989) on bedrock reefs and boulder fields 3 to 20 m deep (Nicholson 1970, Vadas 1972). Across its geographic range, the relative functional importance of *Nereocystis* as a source of surface canopy varies with the occurrence of other species of canopy-forming kelps. In some regions of its range, it is the sole or predominant canopy-forming kelp, while in others it co-occurs with either dragon kelp *Eualaria fistulosa* (formerly *Alaria*) or species of giant kelp *Macrocystis pyrifera* or *M. integrifolia*. The relative abundance of these species varies with respect to both latitude and exposure to ocean swells (Figure 3). In the more protected southern portion of the range, south of Año Nuevo Island (Santa Cruz County, California), *Nereocystis* occurs together with the predominant *Macrocystis*, sometimes forming mixed beds (Foster 1982, Dayton et al. 1984, Dayton 1985, Foster & Schiel 1985, Harrold et al. 1998). From Año Nuevo Island to Alaska, *Nereocystis* is often the sole or predominant canopy-forming kelp on both exposed and protected shores (e.g., Strait of Georgia and Puget Sound, Washington). *Nereocystis* and *Macrocystis* form mixed stands in British Columbia (e.g., western and northern Vancouver Island). *Nereocystis* is the predominant canopy-forming species in south-eastern Alaska, although *Macrocystis* is predominant in some locations along the outer coast (S. Lindstrom personal communication). At the northern end of its range, from north-western Prince of Wales Island to Unimak Island, *Nereocystis* and *Eualaria fistulosa* co-occur regionally, and local beds sometimes alternate between these species through time (B. Konar and S. Lindstrom personal communication). All three kelps co-occur in a few small regions: north-western Prince of Wales Island and Kodiak Islands (M. Norris personal communication). Unattached adult plants (i.e., their holdfasts dislodged from the substratum) have also been found rafting in waters farther south in California (Bushing 1994) and in the Commander Islands in Russia, the westernmost extension of the Aleutian Islands (Selivanova & Zhigadlova 1997).

Evolutionary history

Seaweeds are a polyphyletic group of organisms with varied evolutionary histories. *Nereocystis* is a brown alga (division Heterokontophyta) in the order Laminariales (the true kelps). There are at least 100 species of kelps worldwide (Guiry & Guiry 2010), and this group includes other common

Figure 3 (See also Colour Figure 3 in the insert following page 212.) Geographic distribution of *Nereocystis luetkeana* indicating areas of co-occurrence with two other surface canopy-forming kelps: giant kelp *Macrocystis* spp. and *Eualaria* (formally *Alaria*). Distributional patterns based on personal communications with M. Foster, M. Graham, B. Konar, and S. Lindstrom. Line width proportional to levels of relative abundance across the range of the species.

species, such as *Macrocystis* and *Postelsia* (sea palm). *Nereocystis* is a monotypic genus; traditional taxonomy, largely based on sporophyte morphology, places it within the family Lessoniaceae (Setchell & Gardner 1925). With the advent and increasing accessibility of molecular techniques, the evolutionary relationships among kelp taxa, particularly among the three 'derived' families (Alariaceae, Lessoniaceae, and Laminariaceae) have been the topic of increased scrutiny and debate (Saunders & Druehl 1991, 1993, Coyer et al. 2001). The most comprehensive genetic data to date suggest that *Nereocystis* should be grouped (along with *Macrocystis*, *Postelsia,* and *Pelagophycus*) in a revised Laminariaceae Postels et Ruprecht (Lane et al. 2006). Based on the results of crossing experiments (Lewis & Neushul 1995) and genetic analyses (Lane et al. 2006), *Nereocystis* is thought to be most closely related to *Postelsia*.

There has been some suggestion that *Nereocystis* will hybridize in the laboratory with *Macrocystis* (Lewis & Neushul 1995) in spite of differences in chromosome number (Sanbonsuga & Neushul 1978). However, this is likely to be an artifact of the laboratory and reflective of parthenogenesis or male apogamy rather than actual hybridization (Druehl et al. 2005). No hybrids between *Nereocystis* and *Macrocystis* have ever been found in the field.

Life history

Like all kelp species, *Nereocystis* exhibits alternation of generations between a large, diploid sporophyte stage and a microscopic haploid gametophyte stage (Figure 4). Young sporophytes typically appear in the early spring and grow to canopy height (10 to 17 m) by midsummer. Individuals grow to roughly match the depth at which they settle (i.e., until the pneumatocyst reaches the water surface); this appears to be regulated by a phytochrome-mediated response, such that stipe elongation is inhibited by red wavelengths of light (Duncan & Foreman 1980). *Nereocystis* sporophytes can grow at extremely high rates, up to 6 cm day^{-1} (Scagel 1947). Maximum photosynthesis occurs in

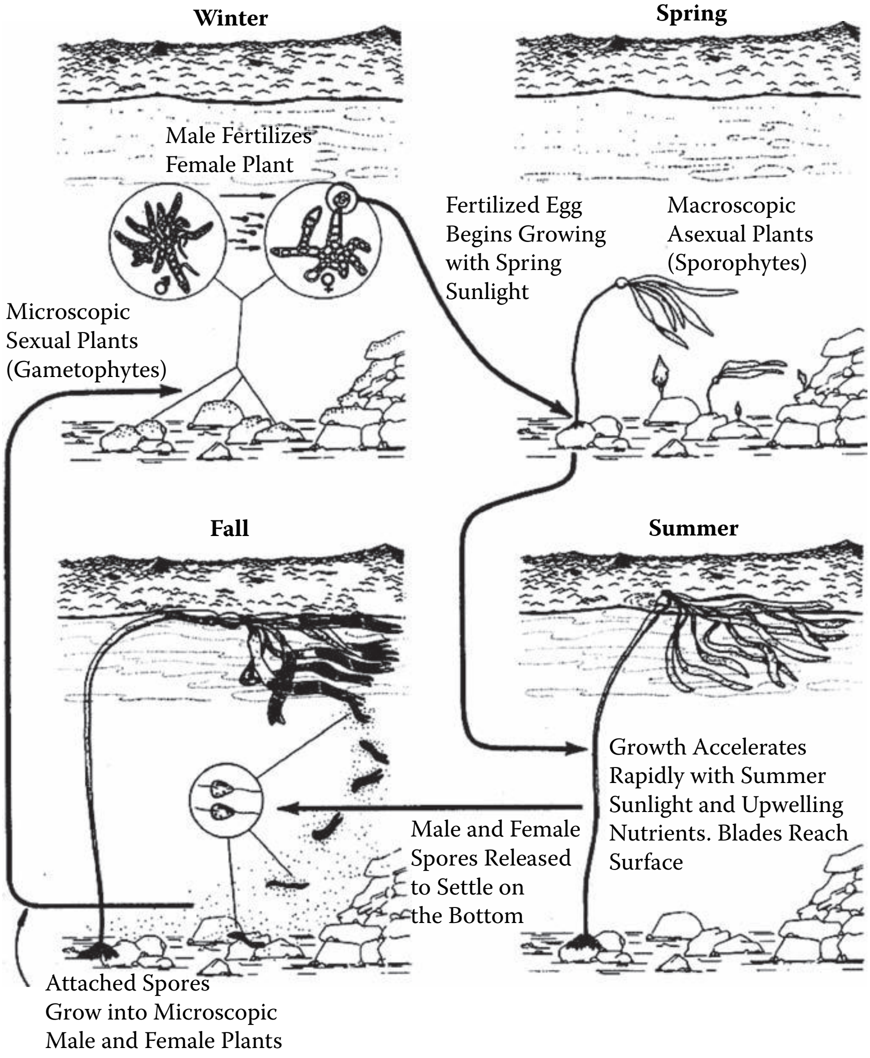

Figure 4 Diagram of the life cycle of *Nereocystis*. (Reproduced from a 1982 report by permission from TERA Corporation, now Tenera Environmental Inc., San Louis Obispo, California.)

summer and early fall, and mortality of *Nereocystis* sporophytes reaches a maximum in the winter, primarily due to dislodgement by winter storms. Lower kelp densities after a storm can also cause surviving individuals to experience increased grazing pressure from sea urchins (Dayton et al. 1992). Each sporophyte produces a single stipe in its lifetime and cannot regrow from its holdfast once the upper stipe is destroyed (Nicholson 1970). Thus, *Nereocystis* is essentially an annual species, although in some populations individuals that are produced late in the season may successfully overwinter and survive a second year (Chenelot et al. 2001). This biennial life history appears to be more common in shallow water populations or protected locations where wave stress is not as great as on the open coast.

Nereocystis sporophytes produce biflagellate haploid spores through reduction division on fertile patches of blades called sori. Sori may be more than 30 cm long and are produced near the proximal end of the blade (Scagel 1947). The maturity of sori therefore increases with increasing distance toward the distal edge of the blade (Nicholson 1970, Walker & Bisalputra 1975, Walker 1980a).

Nereocystis possesses a mechanism for spore dispersal that is rare among kelps: Sori that are releasing (or are about to release) spores abscise from the blade and are released into the water column. Abscission of sori results from a chain of cellular events causing structural weakening (e.g., necrosis of specific tissue layers and dissolution of the cuticle covering the sporangia) in conjunction with the physical force of water motion (Walker 1980b). Within 1 to 4 h of abscission, virtually all spores are released from the sorus (Nicholson 1970, Walker 1980b, Amsler & Neushul 1989).

Spores that successfully settle germinate into microscopic sessile gametophytes, which are uniserate branched filaments. Compared with the conspicuous sporophyte stage, little is known about the ecology of kelp gametophytes. For example, it is unclear how long *Nereocystis* gametophytes persist in the field. There is a distinct seasonality to the reappearance of sporophytes, so it is likely that the production of gametes requires an environmental cue. After 2 to 3 months and exposure to suitable light and nutrients, gametophytes produce oogamous gametes. Vadas (1972) showed that under limited light conditions in the laboratory gametophytes may survive and grow vegetatively for over a year before a change in conditions allows the production of gametes or the growth of very young sporophytes. Evidence of these light-dependent processes suggests that *Nereocystis* gametophytes may act in a manner analogous to a terrestrial seed bank (Santelices 1990, Edwards 2000). Alternatively, seasonality may be imposed by larger-scale phenomena such as strong winter storms and the abiotic environmental changes that accompany them.

Kelp eggs release sexual pheromones that attract sperm (Maier et al. 1987), but the spatial scale over which this mechanism promotes successful syngamy is very low. The density of settling spores, and resulting proximity of male and female gametophytes, is thus critical to fertilization and recruitment success. In giant kelp, spore density must exceed 1–10 spores mm^{-2} for successful recruitment to occur (Reed 1990, Reed et al. 1991). Critical spore density for *Nereocystis* recruitment is not known but is likely to be similar in scale. The recent development of a species-specific method based on polymerase chain reaction (PCR) for detecting microscopic stages (zoospores, gametophyes, and microscopic sporophytes) of *Nereocystis* holds great promise for revealing patterns of spatial dispersion and mortality associated with these phases of the life cycle of the kelp (Fox & Swanson 2007).

Population ecology

Dispersal and population genetic structure

Dispersal of kelp gametes is thought to be negligible. Extruded eggs typically remain attached to the ruptured oogonium on the female gametophyte, and the pheromones that kelp eggs produce (which induce gamete release from male gametophytes and attract sperm to the egg) are only effective when gametes are within about 1 mm of each other (Muller 1981, Maier & Muller 1986). Thus, there are three possible points in the life history of *Nereocystis* when dispersal may occur: as spores, as intact sporophytes, and as detached sori. Detached sori and intact dislodged sporophytes have the potential for long-distance dispersal and gene flow in this species. However, to our knowledge, the relative frequency and scale of dispersal by this mechanism has not been measured.

Nereocystis sporophytes produce an enormous quantity of spores; an average of 2.3×10^5 spores cm^{-2} of sori min^{-1} during initial release has been estimated (Amsler & Neushul 1989), and release may be up to six times faster than those associated with *Macrocystis* (Collins et al. 2000a). Individual plants produce sori on different blades at the same time, but sori mature and are released somewhat synchronously, in pulses that occur every 4–6 days (Amsler & Neushul 1989). Spore production and release occur with a monthly and daily periodicity that varies with geographic location. In British Columbia, *Nereocystis* are thought to release sori only at the beginning of spring tides (Walker 1980b), but near the southern range limit in central California this monthly pattern appears weak or non-existent (Amsler & Neushul 1989). Sori abscission does have a distinct diel pattern in central California. Most abscission occurs in the hours immediately before and after dawn (Amsler & Neushul 1989). Like other kelps (e.g., *Macrocystis*, *Laminaria farlowii*), *Nereocystis* spores are capable of photosynthesis, and although net photosynthesis is low (Watson & Casper 1984), spores should be able to contribute to their own carbon needs. Dawn release may thus reflect an adaptation to maximize photosynthetic opportunity (e.g., to increase viability in the plankton or maximize energy reserves for early germination and growth).

If spores are released from the intact blade or from detached sori drifting through the water column, this mechanism should result in broader dispersal of spores and an increase in the total area over which siblings are distributed (Strathmann 1974, Amsler & Neushul 1989). However, many (or most) spores are likely still retained in the sorus when it arrives at the substratum, which would both concentrate a large portion of siblings spatially and may ensure that most progeny remain near the parent plant (Amsler & Neushul 1989). Kelp spores (e.g., *Macrocystis*) can remain viable in the water column for several days (Reed et al. 1992, Brzezinski et al. 1993) and may be dispersed over long distances by ocean currents (Reed et al. 1988, Norton 1992). In Kachemak Bay, Alaska, *Nereocystis* is only found in the outer bay, so that sporophyte distribution is thought to be driven by estuarine current flow, which acts to prevent dispersal of spores into the inner bay (Schoch & Chenelot 2004).

A population genetic approach is necessary to resolve the spatial scale of population connectivity and would also provide insight into the relative importance of the three potential mechanisms of dispersal. Currently, no published studies of population genetic structure in *Nereocystis* are available.

Spatial and temporal variation in population dynamics

Nereocystis shows high spatial and temporal variability in distribution and abundance patterns, consistent with its annual life history and tendency to colonize recently disturbed areas. For example, in a study of the effects of harvest on *Nereocystis* dynamics, Foreman (1984) found greater interannual variability in abundance in 1-hectare control plots than in plots that had been harvested (see section on historical and current stock assessments beginning on p. 19 for descriptions of available data on spatial and temporal variation in *Nereocystis* cover/productivity across the range of the species).

The reproductive phenology of *Nereocystis* also varies spatially, and it seems that sporophyte recruitment and spore production occur earlier in more northern populations. Burge and Schultz (1973) studied *Nereocystis* in Diablo Cove, California, and documented initiation of new sporophytes from late March through August. Sori were present on blades before they reached the water surface, and complete abscission of sori occurred over a long time: as early as June and as late as March of the following year. More than 1600 km to the north, in Tacoma Narrows, Washington, *Nereocystis* appears to be a strict annual. Sporophytes recruit slightly earlier and more synchronously (early March through June), with peak spore release occurring in August (Maxell & Miller 1996). In the westernmost population in the current distribution of the species (Umnak Island, Alaska), Miller and Estes (1989) observed that sporophytes in July showed characteristics (i.e., size, maturity, and epiphyte cover) that typically reflect individual condition in fall and winter. There was no evidence of a second cohort of smaller individuals, so it seems unlikely that all individuals were second-year plants that had successfully overwintered; earlier recruitment or faster growth of sporophytes provides a more plausible explanation.

Leaman (1980) quantified seasonal variation in sporophyte fertility (number of fertile blades, average sori number and area) in Barkley Sound, British Columbia, from June through October and found that peak fertility occurred in early July, with a smaller peak in September and October. No comparable data on seasonal variation in spore production are available for California populations (according to Collins et al. 2000a).

Abiotic and biotic factors limiting distribution and abundance

Physical factors known to influence the distribution and abundance of subtidal kelp species include irradiance, substratum, sedimentation, nutrient levels, temperature, water motion, and salinity. As pointed out by Dayton (1985), these effects are often difficult to characterize because they seldom act in isolation (e.g., increased water motion may act to increase water turbidity, decreasing irradiance). Moreover, the interactive effects of these factors (or their interaction with biotic ones) may be complex and non-intuitive.

Light Studies of *Nereocystis* in culture suggested that the total quantity of light (photoperiod × intensity) is the single most important factor in the development of both gametophytes and young sporophytes (Vadas 1972). Furthermore, the range of conditions under which vegetative growth is maintained is broader than the conditions necessary for reproduction. In laboratory cultures, gametophytes did not reach sexual maturity under light levels <15 foot candles. Given that light availability is typically well below this threshold in mature kelp forests, it is likely that *Nereocystis* recruitment is light limited in established kelp stands (Vadas 1972).

Temperature Upper thermal limits are often a phylogenetically conserved trait, and thermal tolerance is thought to constrain the southern range limit of many algal species, including *Nereocystis* (Luning & Freshwater 1988). The decline of *Nereocystis* near warm water discharge from the Diablo Canyon power plant (Pacific Gas and Electric Company 1987) supports this idea. Culture studies with *Nereocystis* showed that the thermal conditions that allow sporophyte and gametophyte reproduction range from 3°C to 17°C (Vadas 1972). Much of the Aleutian Islands chain is influenced by the Kuroshio Current, so it seems unlikely that thermal constraints alone could be responsible for the sharp northern/western boundary observed at Umnak Island. Alternatively, light limitation driven by the high fog cover characteristic of the western islands, especially in the summer, may act to prevent spread (Miller & Estes 1989).

Nutrient levels Both spatial and temporal variation in nutrient availability can strongly influence kelp productivity (Dawson 1966, Rosell & Srivastava 1984). The seasonal growth pattern of *Nereocystis* is such that initial growth occurs in late winter and early spring, when organic and inorganic nitrogen levels are relatively high. During the summer months, C:N ratios in *Nereocystis* peak, generally as a result of reductions in the availability and assimilation of nitrogen (Rosell & Srivastava 1985). Like other kelps, *Nereocystis* displays simultaneous uptake of both nitrate and ammonium but shows a preference for nitrate. Ahn et al. (1998) found that nitrate uptake by *Nereocystis* increased linearly with nitrate availability, up to the highest concentration tested (30 μM). In contrast, ammonium uptake rates reached a plateau at availabilities >10 μM. In addition to macronutrients and micronutrients known to influence algal productivity in general (e.g., phosphate, potassium, calcium, magnesium), *Nereocystis* has the capacity to take up other metallic and non-metallic compounds from seawater (Whyte & Englar 1980a,b). What role they may play in *Nereocystis* growth is unknown.

Wave action There is a complex relationship between any benthic alga and the hydrodynamics of its environment. Hydrodynamics can directly affect individual fitness through multiple avenues, such as nutrient uptake rates and gas exchange, direct effects on reproduction and recruitment, as well as flow-induced mortality via dislodgement (e.g., wave action during winter storms is thought to be the main source of mortality for sporophytes, but see Duggins et. al. 2001). *Nereocystis* is relatively resistant to dislodgement compared with other large kelps and is typically found in nearshore habitats characterized by high wave action. This distributional characteristic is especially evident in the southern portion of its geographic range, where it frequently co-occurs with giant kelp. In the northern part of its range, *Nereocystis* survival and distribution show a non-linear relationship with flow, driven by an interaction with herbivory (Duggins et al. 2001). Herbivore abundance typically shows an inverse relationship with wave exposure, and damage by herbivores can compromise the structural integrity of the *Nereocystis* stipe and holdfast. This interaction between physical and biotic stresses is thought to be the reason why northern *Nereocystis* populations are seldom found in habitats with intermediate flow energy; that is, the combination of both high grazing pressure and periodic high drag forces exerted on herbivore-damaged kelp may result in a sharp increase in sporophyte mortality rates.

Nereocystis is a striking exception to the general rule that wave-swept organisms tend to be smaller than sister taxa that occur in calmer waters. This intriguing observation has motivated empirical investigations, beginning in the mid 1970s, that produced a series of highly technical studies of the biomechanics of *Nereocystis* morphology. For example, see Koehl & Wainwright (1977) and Johnson & Koehl (1994) for a consideration of unidirectional flow and Denny et al. (1997) for an analysis of dynamic flow effects. *Nereocystis* also shows dramatic phenotypic plasticity in frond morphology in response to flow. At relatively calm sites, *Nereocystis* produce blades that are wide and undulate with wavy margins, whereas in more exposed habitats blades are narrow, flat, and strap-like. Work involving both laboratory and field transplant experiments demonstrated that this morphological variation is caused by water flow and associated hydrodynamic drag (Koehl et al. 2008). Physiologically, the ruffled blade morph is produced when longitudinal growth along the edge of the blade exceeds the rate of longitudinal growth along the blade midline. The two morphs appear to arise from a trade-off between dislodgement risk and photosynthetic efficiency. The fluttering of ruffled blades may reduce self-shading and enhance interception of light (by orienting perpendicular to current flow) (Koehl & Alberte 1988, Hurd et al. 1997), and water turbulence generated at the blade surface may act to enhance nutrient uptake (Hurd & Stevens 1997), but greater drag will increase the risk of breakage under high flow stress.

Grazers Major grazers of *Nereocystis* include red and purple sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus,* respectively) and red abalone (*Haliotis rufescens*), as well as limpets (e.g., *Collisella pelta*), snails (e.g., *Tegula* spp., *Callistoma* spp.), and various crustaceans (Cox 1962, Nicholson & Briggs 1972, Burge & Schultz 1973). Sea urchin grazing in particular is well known to exert a powerful influence on kelp forest dynamics, and many studies have documented this effect (e.g., Paine & Vadas 1969, Duggins 1980, Pace 1981). When sea urchins are removed from the system, the presence and density of *Nereocystis* sporophytes can increase dramatically. Breen et al. (1976) found that the density and area of *Nereocystis* beds increased following removal of red sea urchins. In a study by Pace (1981) performed in Barkley Sound, British Columbia, *Nereocystis* density increased from 4.6 plants m^{-2} to 13.9 plants m^{-2} in a single year following experimental removal of red sea urchins. Work by Duggins (1980) showed that in the year following sea urchin removal in Torch Bay, Alaska, kelp biomass increased from zero standing crop to roughly 60 kg wet mass m^{-2}, most of which was *Nereocystis*. Increases in the size and density of *Nereocystis* beds near Fort Bragg, California, between 1985 and 1988 were correlated with the commercial harvest of roughly 32,500 t of red sea urchins from areas off the coast of Mendocino and Sonoma Counties (Kalvass et al. 2001). Several studies have also demonstrated that the seaward limit of *Nereocystis* beds may be set by sea urchin grazing (Breen et al. 1976, Pearse & Hines 1979). The capacity of the species for rapid growth under high light conditions permits fast recovery by *Nereocystis* sporophytes when the canopy opens up due to grazing or other disturbance. For example, Foreman (1977a) showed that *Nereocystis* underwent the largest variation in biomass of any algal species over the course of recovery from grazing by green urchins in the Strait of Georgia, British Columbia, and dominated the algal community for a period of 4 yr before declining toward predisturbance levels. A study by Chenelot & Konar (2007) that examined the effects of grazing by the mollusc *Lacuna vincta* on different age classes of *Nereocystis* in Kachemak Bay, Alaska, found that the snail fed significantly more on tissue of juvenile than adult plants, and that snail densities in nature can exceed 1500 m^{-1} on juvenile blades. This apparent preference for young plants, coupled with observation of high but spatially patchy snail densities in the field, led the authors to conclude that grazing by *L. vincta* has the potential to strongly influence the dynamics of local *Nereocystis* populations.

In addition to direct negative effects of grazing, the presence of grazers can have important interactive effects with other biotic and abiotic factors. For example, damage by grazers can weaken the structural integrity of the *Nereocystis* stipe and holdfast and increase an individual plant's vulnerability to wave action. Koehl & Wainwright (1977) reported that 90% of detached single individuals had broken at a flaw in the stipe. While this damage appeared to be caused by herbivore grazing, no conclusive evidence supporting this anecdotal connection could be found. Herbivory can also alter the competitive hierarchy among kelps and other macroalgae (Paine 2002), and the presence of herbivores may positively affect *Nereocystis* by decreasing competition with other algal species. In the absence of herbivory, species of understory and turf algae such as foliose reds (*Botryoglossum farlowianum*, *Polyneura latissima*) and midwater canopy species (*Laminaria* spp., *Pterygophora californica*, *Eisenia arborea*) can reach high levels of abundance and prevent the recruitment of *Nereocystis* through competition for primary space and overshadowing (discussed in Collins et al. 2000b). Such effects have been observed in association with a number of different mechanisms, such as after mass disease-related mortality of sea urchins in Carmel, California (Pearse & Hines 1979), the introduction of sea otters (predators of urchins and abalone) in Torch Bay and Surge Bay, Alaska, and Diablo Cove, California (Duggins 1980, Gotshall et al. 1984, Estes & Duggins 1995), and the commercial harvest of red sea urchins near Fort Bragg, California (Collins et al. 2000b). The beneficial effects of sea urchin grazing for *Nereocystis* may be particularly important in areas of heavy scour, and unstable substrata where the rapidly colonizing red algae that potentially outcompete *Nereocystis* are often the predominant component of stands of macroalgae (Duggins 1980). Thus, the net effects of herbivory on *Nereocystis* beds will be driven by both the abundance and feeding preferences of grazers and the nature of competitive interactions between *Nereocystis* and other species of algae with which it co-occurs at a given location. Furthermore, although grazing is clearly an important driver of *Nereocystis* population dynamics, the effects of different grazer species on per capita rates of *Nereocystis* growth, survival, and reproduction are largely unknown. Because of their size, kelp gametophytes may be vulnerable to mortality from grazers, but this interaction has not been examined quantitatively.

Competition As alluded to in this discussion, competition is another major driver of *Nereocystis* distribution, both within and across sites. *Nereocystis* is generally thought to be an opportunistic kelp that can rapidly colonize disturbed sites but is usually outcompeted by competitively perennial species in the absence of disturbance (Dayton et al. 1984, Dayton 1985). Where bull and giant kelp co-occur, *Nereocystis* is typically only found in more exposed areas where *Macrocystis* abundance is low and understory kelps are sparse (Figure 2). *Nereocystis* also displays temporal dynamics that are consistent with an r-selected species (e.g., rapid population growth in response to disturbance and increased light availability, eventual replacement by other species; Foreman 1977b).

Epiphytes A wide variety of different epiphytic algae and invertebrates colonize *Nereocystis*; over 50 species of epiphytic algae have been documented on *Nereocystis* blades and stipes, often showing distinct patterns of vertical distribution (Markham 1969). Common algal epiphytes include filamentous species of *Ulva, Enteromorpha,* and *Antithamnion* and the foliose red alga *Porphyra nereocystis*. As the species epithet implies, *P. nereocystis* is a common epiphyte on the stipe of *Nereocystis* (and occasionally other laminarian kelps) and displays a life history that synchronizes reproduction and recruitment with its host (Dickson & Waaland 1984, 1985). Epiphyte cover on *Nereocystis* sporophytes increases over the summer and through fall and winter and can cause strong reduction in photosynthesis through direct shading of blades. At high levels of epiphyte cover, this added weight may overcome the buoyancy of the pneumatocyst and cause the entire alga to sink to depths where light intensity is lower and blades are more likely to be in direct contact with grazers (Collins et al. 2000a). Epiphyte load leads to increased tattering of blades and may increase the likelihood of complete detachment during high wave forces due to increased drag (Foreman 1970). Some blade tissue may also be inadvertently lost to fish feeding on epiphytic plants or animals (e.g., Hobson & Chess 1988). No estimates of either sporophyte mortality or reduction in photosynthesis and productivity due to the direct or interactive effects of epiphytes on *Nereocystis* are currently available.

Disease The only known parasitic algae that commonly infects *Nereocystis* is *Streblonema* sp., a brown alga that apparently causes distortions of the stipe ranging from galls to extended rugose areas. These deformations can weaken the stipe and could result in breakage during exposure to strong surge or storm conditions. *Nereocystis* does not appear to be susceptible to black rot disease or stipe blotch disease, conditions that affect other brown alga and can result in substantial loss of biomass through degradation and abscission of stipes and blades (Collins et al. 2000a).

Community ecology and its role in coastal marine ecosystems

Direct and indirect interactions with other species

Macroalgae can interact directly with other species by competing for limited resources (e.g., light, space, nutrients), providing food for herbivorous grazers and detritivores, and providing habitat for other algae, invertebrates, and fishes. Macroalgae can also indirectly influence other species through mechanisms that include modification of water flow and the delivery of larvae and other plankton, harboring of prey and predators of other species in a community, and trophic cascades (i.e., fueling grazer or detritus-based trophic pathways). Whereas such interactions have been the focus of numerous studies of *Macrocystis*, similar studies involving *Nereocystis* are few. Nonetheless, the diverse ecological functions that have been attributed to *Nereocystis* can have direct implications for the variety of ecosystem services that *Nereocystis* provides to human societies (Table 1).

Macroalgae As described in the section on biotic factors that limit its distribution and abundance, *Nereocystis* appears to be competitively inferior to many other algae (Foster & Schiel 1985 and others cited previously). This conclusion is based in part on the ephemeral occurrence of individual plants and whole forests and the small holdfast and narrow morphology that constrain its usurpation of space on a reef and attenuation of light, respectively. As such, the impact of *Nereocystis* on other macroalgae is thought to be limited, although more research on this topic is warranted. One exception to this general conclusion is the facilitative effect *Nereocystis* has for epiphytes (see section on epiphytes). Whether modification of water flow by *Nereocystis* on reef habitats (diminishing current speed and turbulence) also facilitates or impairs the growth, survival, and replenishment of other macroalgae remains unclear.

Invertebrates A variety of small invertebrates uses the stipe and canopy of *Nereocystis* for food and habitat (e.g., sessile invertebrates such as bryozoans, especially *Membranipora membranacea*, hydroids, and barnacles, and small mobile grazers such as isopods, caprellid amphipods, and snails; McLean 1962, Burge & Schultz 1973, Foster et al. 1979, Foster 1982, Gotshall et al. 1984, 1986). The benthic invertebrate assemblage associated with *Nereocystis* is similar to that associated with other annual kelp. Gotshall et al. (1984) documented lower invertebrate abundances around *Nereocystis* than *Macrocystis*, with the notable exception of red and purple sea urchins, which were more than twice as dense under *Nereocystis* beds. Also, like giant kelp, the holdfast of *Nereocystis* provides habitat for a large number and diversity of small invertebrates, including brittle stars,

Table 1 Summary of ecosystem functions and services provided by bull kelp *Nereocystis luetkeana*

Ecosystem function	Ecosystem service
Trophic functions	
Primary production	Source of carbon sequestering
Fuels secondary production: grazers (crustaceans, gastropods, echinoderms)	Production of culturally and recreationally important species (abalone), minor harvest for recreational and commercial consumption by humans
Fuels secondary production: detritivores (crustaceans, gastropods, echinoderms)	Production of commercially fished species (abalone, sea urchins), harvested for commercial mariculture of abalone
Fuels tertiary production: invertivores	Production of commercially fished species (crabs, fishes)
Structural functions	
Biogenic 3-dimensional habitat	Provides structural framework for nearshore ecosystems
Source of habitat for epiphytes	Increased local species diversity
Source of recruitment and nursery habitat for juvenile invertebrates and fishes	Production of recreationally and commercially fished species (rockfishes, salmon)
Physical structure dampens inshore swell and turbulence	Reduces swell and coastal erosion
Ecosystem connectivity	
Export of primary production to coastal marine ecosystems (sandy beaches, rocky intertidal, offshore soft-bottom and submarine canyons)	Fuels secondary production of detritivores in other coastal ecosystems

Note: Supporting documentation is provided in the text.

crabs, and small abalone (Andrews 1925), and may serve an important nursery function for juvenile invertebrates (sensu Beck et al. 2001), although this possibility has not been rigorously tested. Calvert (2005) and Siddon et al. (2008) conducted the only large-scale (1500-m^2) manipulations of the presence of *Nereocystis* canopies to examine the effect on the abundance of invertebrate species. They found no effects of canopy removal on invertebrates distributed in either the surface or bottom portion of the water column. However, their sampling was limited to collectors (light traps and standardized monitoring unit for recruitment of fishes [SMURFs]), not visual surveys.

Fishes Because of the commercial and recreational value of fishes that inhabit shallow rocky reef habitats throughout the western coast of North America, a great deal of research has been done on the relationships between macroalgae and fishes. Again, much of this research has focused on interactions between fishes and the giant kelp *Macrocystis* spp., and far less attention has been given to *Nereocystis*. Nonetheless, a few studies have described the relationship between fishes and *Nereocystis* throughout its range. Like other taxa, the relationships between fishes and *Nereocystis* can be divided into trophic and structural interactions and between the juvenile and adult stages.

The strongest relationships between macroalgae and fishes reflect the importance of habitat structure created by macroalgae for the juvenile stages. Although a number of studies have described the importance of algal structure as habitat for larval settlement and refuge from predators (see reviews by Carr & Syms 2006 and Steele & Anderson 2006), almost all of this work has focused on *Macrocystis*. Our understanding of the importance of *Nereocystis* for the recruitment of juveniles to populations of adult reef fishes suffers from a lack of studies targeting this relationship throughout the range of *Nereocystis*. In the few places and cases it has been examined, recruitment of several species of fishes, most notably the rockfishes (genus *Sebastes*), appears to increase in, or is associated with, the presence of *Nereocystis*.

Five examples of observational studies of the association of juvenile fishes with *Nereocystis* are particularly noteworthy. One includes the occurrence of recently settled copper rockfish *Sebastes caurinus* in the canopy formed by forests of *Nereocystis* in the Strait of Georgia, between Vancouver

Island and mainland Canada (Haldorson & Richards 1987). Haldorson and Richards concluded that *Nereocystis* forests were "especially important habitat" for very young copper rockfish that had recently settled into shallow reef habitats. These young fish eventually migrated down plants to the reef habitat. Carr surveyed fish assemblages associated with *Nereocystis* forests along the central coast of Oregon. Very high numbers of juvenile rockfishes, including copper (and perhaps quillback *Sebastes maliger*), and fewer juvenile black (*S. melanops*) rockfish were observed both in the canopy and on the bottom at multiple forests (M. Carr, unpublished data). Similarly, Bodkin (1986) observed aggregations of juvenile rockfishes (various species combined) at mid-depth and on the bottom of a *Nereocystis* forest in central California. In that study, it is unknown whether the fishes use the canopy habitat specifically because that portion of the water column was not sampled. Leaman (1980) mentioned that juvenile stripe surfperch *Embiotoca lateralis* were more abundant within the *Nereocystis* forest than in habitat adjacent to the forest. Comparison of densities of juvenile and adult fishes (primarily rockfishes and Pacific cod *Gadus macrocephalus*) among shallow rocky reefs that varied in the occurrence and density of *Nereocystis* and understory kelps along the coast of south-central Alaska revealed higher fish densities in the presence of *Nereocystis* (Hamilton & Konar 2007).

Central to determining whether *Nereocystis* forests are of particular importance to the growth and survival of juvenile fishes is determining whether the forest habitats contribute disproportionately to the number of juveniles that survive to become adults (i.e., 'nursery habitat' *sensu* Beck et al. 2001). In addition, the most direct evidence of the effect of kelp forests on the local recruitment of reef fishes is from experimental manipulations of the presence of giant kelp (e.g., Carr 1989, 1991, 1994). To date, only three studies have manipulated *Nereocystis* in attempts to assess its effect on recruitment of juvenile fishes (Leaman 1980, Calvert 2005, Siddon et al. 2008). All three studies identified effects on adult fishes, especially small cryptic species, but none detected strong effects on the density of young recruits as described by the observational studies mentioned. In addition to the juveniles of these rocky reef-associated fishes, juveniles of various species of salmon are also frequently observed schooling through, and associated with, stands of macroalgae. One example includes frequent encounters with juvenile pink (*Oncorhynchus gorbuscha*), coho (*O. kisutch*), and chum salmon (*O. keta*) associated with stands of *Laminaria saccharina* in south-eastern Alaska (Johnson et al. 2003), and another is the significantly higher density of juvenile coho and Chinook salmon (*O. tshawytscha*) associated with *Nereocystis* beds along the Washington coast of the central and western Strait of Juan de Fuca (Shaffer 2002).

Information on the association of adult fishes with *Nereocystis* forests is based largely on four observational studies broadly distributed across the geographic range of the alga. Bodkin (1986), Leaman (1980), Dean et al. (2000), and Calvert (2005) described the fish assemblages associated with *Nereocystis* forests in central California, British Columbia, south-eastern Alaska, and Prince William Sound, Alaska, respectively. Because of the close association of kelps with rocky habitat and because the presence of *Nereocystis* forests is highly seasonal, the extent to which the structure of fish assemblages (i.e., diversity and relative abundance of species) is related to *Nereocystis* or the rocky reef habitat is unclear. Bodkin (1986) compared fish assemblages between *Nereocystis* and *Macrocystis* forests but did not compare reefs with and without *Nereocystis*. Leaman (1980) compared reefs with and without *Nereocystis* and noted that three benthic species were particularly associated with the *Nereocystis* plants: the sculpin *Synchirus gilli*, the snailfish *Liparis* sp., and the blenny *Phytichthys chirus*. All three are small (<10 cm length) cryptic species that sit directly on the blades and stipes of the alga. In addition, the tubesnout *Aulorhynchus flavidus* was thought to be influenced by the presence of *Nereocystis* because it deposits its eggs directly on the pneumatocysts. Dean et al. (2000) compared fish assemblages among nearshore environments, including a variety of algal habitat. They found distinct fish assemblages associated with habitats of different vegetation and exposure; the most abundant benthic fishes within eelgrass beds were juvenile Pacific cod (*Gadus macrocephalus*), greenlings (Hexagrammidae), and gunnels (Pholidae), whereas pricklebacks

(Stichaeidae) and sculpins (Cottidae) dominated in *Agarum-Laminaria* headland and bay habitats, and kelp greenling and sculpins were numerically dominant in *Nereocystis* beds. Gunnels were less abundant in *Nereocystis* beds than elsewhere. Thus again, the addition of *Nereocystis* to the mix of vegetation habitats in a region was correlated with greater regional fish diversity.

Long-term manipulative experiments that create reefs with and without kelp forests are the only definitive way to determine the extent to which a fish assemblage is influenced by the presence or abundance of kelp (e.g., Carr 1989). Leaman (1980) conducted short-term manipulations of *Nereocystis* and found that effects of removal of the canopy varied between midwater and benthic fishes and whether the removal was conducted at the edge or middle of the forest. Removal of the canopy near the edge of the bed had little effect on the abundance of benthic species but decreased the abundance and diversity of neritic species. In contrast, removal of the canopy in the middle of the bed increased the density of neritic species and decreased both the abundance and the number of benthic species. Because neritic species feed on plankton transported across reefs, removal of the canopy from inner portions of the bed may have increased the transport and delivery of food to these species. Thus, this study indicated that both benthic and neritic fish assemblages responded to the removal of a *Nereocystis* canopy, and that differences in the response of the two assemblages to canopy removal depended on the location of plant removal within a forest.

Calvert (2005) and Siddon et al. (2008) also conducted two large-scale manipulations of the presence of *Nereocystis* canopy and the subcanopy formed by lower-growing algae (*Laminaria*). They found that fish abundance was greatest in plots with both canopy and subcanopy present, and that the removal of the canopy decreased the local abundance of fishes. However, as Leaman (1980) found, this effect varied between the benthic and neritic fish assemblages. On manipulation of the kelp canopy, significantly greater abundance and biomass of benthic fishes occurred at sites with *Nereocystis* than sites without. Juvenile benthic fishes from the families Pholidae, Cyclopteridae, and Hemitripteridae at sites with *Nereocystis* canopy were twice as abundant and had an estimated biomass more than four times that of fishes observed at canopy removal sites (Siddon et al. 2008). In contrast, a direct negative effect of *Nereocystis* was observed for schooling fishes; six times more schooling fishes (juvenile Pacific cod *Gadus macrocephalus* and walleye pollock *Theragra chalcogramma*) were observed at sites without a canopy kelp. These effects varied seasonally, with the influence on neritic fishes limited to the summer.

In general, where *Nereocystis* and *Macrocystis* forests co-occur, *Nereocystis* forests appear to support lower densities of reef fishes than those associated with *Macrocystis*, but the fish assemblages associated with the two forest types differ somewhat, suggesting that regional fish diversity is increased in nearshore waters where both *Nereocystis* and *Macrocystis* forests co-occur. Both Leaman (1980) and Bodkin (1986) compared fish assemblages between nearby *Nereocystis* and *Macrocystis* forests. Bodkin found that the overall composition of the fish assemblages was generally similar between the forest types; however, the density of many species was generally greater in the *Macrocystis* forest. Leaman (1980) also found greater fish densities in *Macrocystis* forests, but noted that the benthic fish assemblages associated with the two forest types were "decidedly different," with sculpins disproportionately abundant in the *Nereocystis* forest. Both Leaman (1980) and Bodkin (1986) noted greater abundance and representation of neritic species in *Macrocystis* than *Nereocystis* forests. Although based on limited observations, these results suggest that fish diversity is increased in nearshore waters where both *Nereocystis* and *Macrocystis* forests co-occur.

Fishes may benefit from trophic interactions associated with kelp forests as well, by feeding on (1) increased numbers of prey that graze directly on the *Nereocystis* plants (e.g., snails and amphipods), (2) prey that feed on detritus produced by the canopy that detaches and falls to the floor of the forest, or (3) prey associated with the algae (e.g., juvenile rockfishes as described). However, no studies have examined this situation specifically with respect to the presence or abundance of *Nereocystis*.

Interactions with other ecosystems

The extent of exchange of resource subsidies between biological communities is an area of great current interest in ecosystem ecology. Given the massive productivity of *Nereocystis* sporophytes, bull kelp populations are likely to have considerable impacts on adjacent habitats and ecosystems through the allochthonous export of biomass (Colombini & Chelazzi 2003). *Nereocystis* production can be exported to other marine ecosystems (e.g., marine canyons, sandy beaches, rocky intertidal areas) as detritus or when blades or entire thalli are dislodged or broken from their holdfast. Allochthonous input from detached subtidal algae is known to be particularly important in ecosystems with limited primary production (Kim 1992, Vetter 1995, Harrold et al. 1998) and can influence community dynamics by changing the bacterial community (e.g., Tenore et al. 1984) and providing refugia (e.g., Norkko et al. 2000) and a food source for invertebrates (e.g., Pennings et al. 2000). The probability that drifting *Nereocystis* blades or thalli are retained in a habitat varies spatially, likely with local oceanographic features and with substratum characteristics (e.g., Orr et al. 2005). Commensurate with the rapid growth of *Nereocystis*, decomposition of lamina tissue is relatively rapid (Smith & Foreman 1984), although the impact of *Nereocystis* in detrital pathways has not yet been quantified. A study by Mews et al. (2006) of beach wrack decomposition found that *Nereocystis* decay rates were considerably higher than those of other common wrack species (*Macrocystis integrifolia, Fucus* spp., *Ulva* spp., and *Phyllospadix* spp.) in Barkley Sound, British Columbia. These results suggest that energetic resources exported from *Nereocystis* beds in the form of drift kelp may be quickly broken down and assimilated on arrival in other marine ecosystems.

Human activities and management

Harvest

Nereocystis has been harvested for human consumption, agricultural purposes, and for use as mariculture feed. The thick central stalk is pickled and marketed as a speciality food product, and the dried parts are used for arts and crafts (Kalvass et al. 2001). *Nereocystis* is very similar to wakame (*Undaria pinnatifida*) used in traditional Asian cooking and may have potential as a culinary substitute (Malloch 2000). It is thought to be a blood-cleansing product by Koreans, and new mothers traditionally eat it every week for a year after giving birth (Malloch 2000). Bull kelp tissue has been harvested for use in the production of liquid fertilizer and as feed in abalone mariculture (Kalvass et al. 2001). Unlike *Macrocystis*, female herring will not deposit their eggs on fronds of *Nereocystis*, and as such it is not used in the spawn-on-kelp (SOK) industry. SOK is a speciality seafood product that consists of kelp fronds covered in herring roe and then stored/preserved in brine. Popular in Japan, where it is known as komochi (or kazunoko) konbu, SOK is produced commercially in enclosed bays or inlets called ponds. Harvest kelp blades are strung across the pond on lines, and herring are then introduced to or given access to the ponds for egg deposition.

In contrast to *Macrocystis*, for which harvesting involves removal of tissue from the upper 4 ft of canopy and leaves the rest of the plant essentially intact and capable of continued vegetative growth and reproduction, harvesting of *Nereocystis* often involves the removal of the pneumatocyst and associated blades (Figure 2). By removing most of the photosynthetic and meristematic tissue of an individual plant, this method of collection eliminates the potential for further vegetative growth and eventually kills the plant by removing its source of buoyancy, causing the stipe to sink to the substratum (Mackey 2006). As a result, if collection occurs prior to the release of reproductive spores, plants harvested in this manner do not contribute reproductively to the maintenance of the populations of which they are a part. Collection involving pneumatocyst removal can thus have immediate, dramatic, and long-lasting effects on the extent of *Nereocystis* canopy cover in harvested beds. To avoid these outcomes, it has been recommended that harvesting (1) involve only the removal of distal portions of the fronds to allow for vegetative regrowth of adult plants and (2) be timed according to the reproductive schedules of the plants such that it does not occur before the production and release of reproductive spores (Wheeler 1990). Admittedly, more data on these schedules will need to be collected to determine the timing and predictability of reproductive events associated with local *Nereocystis* populations.

In further contrast to giant kelp, for which numerous harvesting-related studies have been performed, the effects of harvesting on *Nereocystis* remain largely unexplored. The provincial government of British Columbia funded two studies of the effects of *Nereocystis* harvesting on kelp forest ecology (Wheeler 1990). In an earlier study performed by Foreman (1984), no significant harvesting effects could be detected on recruitment and regrowth of the beds in subsequent years. The impact of harvesting was simulated by removing all *Nereocystis* sporophytes from within 100-m^2 experimental plots at Malcolm Island and comparing abundance in those plots in subsequent years with control plots where no harvesting occurred. Whereas the results suggested that harvesting had no measurable effect on temporal patterns of plant density or mean plant biomass, the limited replication and short duration of the experiment (two to three plots, 6 yr total with 2 yr of postmanipulation monitoring) severely limit the spatiotemporal scale of inference. Foreman pointed out that harvesting by hand could allow for selective removal of stipes from plants only after their sori had been released. It is now known, however, that *Nereocystis* blades will continuously produce sori until the plant dies. Given this fact, data on rates of sori production during the course of the growing season would be needed to identify the optimal timing for lamina harvest that minimizes impacts on lifetime sori production of harvested plants. In a study of harvest involving partial removal of fronds rather than complete removal of the pneumatocyst, Roland (1985) explored the influence of timing of harvest and extent of tissue removal on sporophyte growth and reproduction. *Nereocystis* sporophytes growing in a bed near Victoria, British Columbia, had laminae cut 30 cm above the pneumatocyst once, every 30 days, or not at all (unharvested control). Harvest via partial removal of laminae did not significantly increase mortality of plants relative to unharvested controls, but postharvest lamina production and the proportion of blades bearing reproductive sori were significantly reduced in both harvest treatments (Roland 1985). These effects could influence both the amount of canopy biomass available as habitat and as detritus for associated fish and invertebrate communities and the number of reproductive propagules contributing to recruitment to the bed in subsequent years.

The history of harvest, current and historical stock assessments, and current harvest and management of bull kelp are described next, organized by the region under which management occurs (i.e., British Columbia and in the United States by state).

California

History of harvest Kelp has been harvested commercially off the California coast since the early 1900s. The vast majority of this collection involved *Macrocystis*, extracts from which were used in the manufacturing of explosives, livestock and mariculture feed, and algin. ISP Alginates (formerly Kelco), the largest commercial kelp-harvesting operation in California, accounts for at least 95% of the annual harvest in the state. The company has been in operation since 1929 and by 2002 had acquired lease rights to 15 beds (~28 miles^2) from Monterey Bay to Imperial Beach. Approximately 22 other harvesters held licenses to collect kelp in 2002 (Little 2002). Like ISP Alginates, nearly all of these firms also targeted giant kelp.

In contrast to *Macrocystis*, there was essentially no targeted harvesting of *Nereocystis* in California until the 1980s. Prior to that time, small amounts of incidental harvesting of *Nereocystis* likely occurred during the harvest of giant kelp in mixed-stand beds, but amounts were never quantified. Abalone International, a Crescent City mariculture company, began collecting *Nereocystis* from a region between Point St. George and the Crescent City Harbor in 1988 and received exclusive lease privileges from the California Department of Fish and Game (CDFG) for collection in bed 312 in 1997 (Kalvass et al. 2001). Based on estimates of local *Nereocystis* abundance in this region, their harvest limit was set at 821 t yr^{-1} (Kalvass et al. 2001). Peak harvest by this firm was only 149 t in 1999, and collection dropped substantially thereafter, with only 11 and 44 t landed in 2000 and 2001, respectively (harvesting statistics are given in a table in Collins et al. 2000a). This decline has been attributed to decreasing demand rather than reduced availability of the resource (Kalvass et al. 2001). As of 2002, only 3 of the state's 13 *Nereocystis*-dominated beds were open to harvest, and only 1 is currently leased to a commercial harvesting operation (bed 312, to Abalone International).

Historical and current stock assessment The first survey of kelp abundance in California that recognized *Nereocystis* was part of a larger mapping effort spanning the Gulf of Alaska to Cedros Island (Baja California) between 1911 and 1913. This work, overseen by Dr. Frank Cameron, was undertaken by the U.S. Bureau of Soils to investigate the potential use of kelps as a source of potash fertilizer (Cameron 1912). Historical records of *Nereocystis* abundance are limited because subsequent surveys often did not differentiate between *Macrocystis* and *Nereocystis*. In addition, because most of these subsequent surveys were motivated by a desire to map the distribution of the more economically valuable *Macrocystis*, few were conducted in northern areas of the state where *Nereocystis* predominates. Current estimates of the sizes of *Nereocystis* populations in northern California are based largely on surveys performed in 1989 and 1999 and on information from the Crescent City area (Del Norte County) provided by Abalone International (Kalvass et al. 2001). While the 1912 and 1989 surveys estimated roughly 6.5 $miles^2$ of *Nereocystis* canopy north of Point Montara, the 1999 survey indicated a decline of approximately 42% in kelp coverage in the area between Point Montara (San Mateo County) and Shelter Cove (Humboldt County) (Kalvass et al. 2001). This apparent decline, which runs counter to observations of extensive beds in this region in late 1999, may be attributable in part to (1) the timing of the 1999 survey, which occurred after a major storm; (2) improved interpretation methods for aerial photos; or (3) natural fluctuations in kelp bed coverage and density (Kalvass et al. 2001). On a more local level, the Crescent City harvesting operation conducted a 1996 survey of *Nereocystis* abundance in bed 312 as part of their harvesting lease agreement with CDFG. This yielded an estimate of 5475 t of *Nereocystis* in the 205 acres of bed 312 between Point St. George and Whaler Island.

No recent *Nereocystis* surveys have been done in central California. Results of the 1912 survey suggested that 32% of the 17.55 mi^2 kelp canopy in this region was associated with *Nereocystis* (Kalvass et al. 2001). In central California, *Nereocystis* seems to be outcompeted by *Macrocystis* and is generally restricted to areas (1) on the outer fringes of giant kelp beds, (2) within the surge zone, or (3) from which giant kelp has been temporarily removed by disturbance associated with winter storms or strong waves. Evidence of the temporally dynamic nature of *Nereocystis* abundance comes from Diablo cove, where density levels declined from 200 t $acre^{-1}$ in 1975 to 4.8 t $acre^{-1}$ in 1982 (Kalvass et al. 2001).

Management and recent harvest California's kelp bed management, a responsibility of the CDFG, has focused mostly on *Macrocystis*. Collection of kelp for commercial purposes requires a 1-yr, \$100 license, and harvesters are required to keep collection records (discussed in the next paragraph). Kelp beds may be leased from the State Land Commission for up to 20 years with a deposit of no less than \$40 $miles^{-2}$. Leased areas may not exceed 25 $miles^2$ or 50% of the total kelp resource, whichever is greater (Mackey 2006). There is a royalty for edible seaweeds of \$24 wet t^{-1} harvested from waters other than San Francisco Bay and Tomales Bay (Mackey 2006). No collection is allowed in marine life refuges or specially designated aquatic parks. If *Nereocystis* is collected for human consumption, the harvest limit is 2 t each year, and the entire plant must be harvested. Collection is to be performed by cutting, and harvesting must be at a depth of less than 4 ft below the water surface (Hillmann 2005). Collection for personal and scientific use requires a permit and is limited to 10 pounds wet weight per permit (Mackey 2006). Personal, non-commercial harvest is prohibited in marine life refuges, marine reserves, ecological reserves, national parks, or state underwater parks (Mackey 2006).

All commercial harvesters are required to keep records of the weight, species, collector, and location of harvest and report these figures to CDFG on a monthly basis (Kalvass et al. 2001, Mackey 2006). Although these harvest summary data have been collected regularly since 1915, routine and formal stock assessments of the state's kelp resources have never been performed. CDFG conducts aerial surveys of California kelp beds only periodically, and while many commercial harvesters (e.g., ISP Alginates) conduct additional aerial surveys of their own (probably with greater frequency and precision), the resulting data are often proprietary and not available to the public or management agencies (Little 2002). As such, although the Fish and Game Code (§6654) gives the CDFG the authority to close a kelp bed to harvest for up to 1 yr if it is determined that the bed is being damaged by collection, the information necessary to detect detrimental impacts of harvest on kelp resources is largely unavailable (Kalvass et al. 2001).

Given these management resources, the CDFG commission took the following formal precautionary steps to protect kelp beds in northern California (especially *Nereocystis*) in 1996. First, the kelp bed-numbering system initiated in 1915 for beds in southern and central California was extended by adding a 300-series designation for kelp beds north of San Francisco (Kalvass et al. 2001, Little 2002). These beds are composed primarily of *Nereocystis*. Prior to this action, because of the lack of formal CDFG recognition, any northern bed could have been harvested for commercial purposes. Second, beds 303–307 were closed to future commercial harvest. Finally, collection in the remaining beds in the 300 series was limited to a maximum harvest of 15% of the biomass as determined by a CDFG-approved annual survey conducted by the lessee. In 2001, the commission added the following additional restrictions (Kalvass et al. 2001). First, beds 301, 302, 310, and 311 were closed. Harvesting of *Nereocystis* was restricted north of Point Arguello by California code of regulations title 14, section 165(c)(4) (Monterey Bay National Marine Sanctuary 2000). Second, harvest was restricted from April 1 through July 31 within the Monterey Bay National Marine Sanctuary. Third, harvesters were required to have a commission-approved harvest plan prior to taking kelp with a mechanical harvester in open beds north of Santa Rosa Creek (San Luis Obispo County). Finally, the commission assumed the authority to designate open beds, or portions thereof, as harvest control areas where harvest is limited for a specific period of time.

As of 2006, there were five active commercial permits in California for *Macrocystis* harvest and none for commercial harvest of *Nereocystis* (Mackey 2006). A 3-yr experimental kelp-harvesting permit has been granted to The Nature Conservancy to study the effects of giant kelp harvesting on associated fish assemblages (Mackey 2006). Very little is known about the nature and magnitude of recreational harvest (Little 2002).

Oregon

History of harvest The only recent documented commercial harvest of *Nereocystis* in Oregon occurred from 1988 through 1992, when a company collected approximately 70 t of tissue from kelp beds associated with Orford Reef in southern Oregon (Kalvass et al. 2001, Mackey 2006). A 5-yr experimental lease granted to a different commercial entity by the Oregon Department of State Lands (DSL) in 1996 expired in 2000 with no harvest ever having occurred.

Historical and current stock assessment In 1954, Waldron conducted perhaps the first formal survey of *Nereocystis* distribution and abundance focused specifically on the coast of Oregon (Waldron 1955). Using aerial surveys of the coastlines of Lincoln, Coos, and Curry Counties, he noted that beds were typically located within 1 mi of the shore in less than 60 ft of water and tended to be concentrated in areas protected from prevailing winds. Beds were small or absent on the seaward sides of reefs and along exposed sections of headlands. Across the three survey areas, he estimated

3704 total acres of kelp beds, of which 1766 acres were classified as being of moderate or high density and accessible for harvest. Over 70% of the total acreage was located in Curry County, with the bed at Orford Reef accounting for over 20% (791 acres) of this total. A team from the Oregon Department of Fish and Wildlife surveyed *Nereocystis* beds on five subtidal reefs in Oregon (Orford, Blanco, Redfish Rocks, Humbug Mountain, and Rogue Reefs) in 1996, 1997, and 1998 (Fox et al. 1998). They compared kelp biomass estimates derived from three measures: weights of individual plants, plant density derived from canopy percentage cover estimates, and total canopy area at the ocean surface. The Orford Reef bed was consistently the largest (estimated biomass between 6454 and 3442 t), but interannual variation in bed size was high, and no consistent temporal trends were apparent. The results suggested that estimates of the surface area of kelp beds might not be an accurate proxy for annual biomass. Across all five reefs, total surface area ranged from 179 to 371 ha, and estimated biomass fluctuated between 8137 and 16,583 t.

Management and recent harvest The DSL has jurisdiction over submerged subtidal lands (any land "lying below the line of ordinary low water of all navigable waters within the boundaries of this state") and can issue permits for commercial leasing of state-owned portions of these lands (Mackey 2006). Prior to October 2008, up to 40 miles of submerged land could be leased to a single individual for a period of no more than 50 yr with no stated restrictions of the amount of kelp that may be harvested during the lease period. However, on 14 October 2008, the State Land Board approved a rule change that effectively prohibits the harvest of kelp and other seaweed for commercial purposes from state-owned submerged lands [OAR 141-125-0120(13)]. Persons collecting <2000 pounds of kelp yr^{-1} from these lands for the purpose of personal consumption do not require a lease. No commercial collection is permitted within the Oregon Shore Recreation Area, and kelp harvesting is prohibited in 12 specially managed marine areas: Haystack Rock Marine Garden (Cannon Beach), Cape Kiwanda Marine Garden (Pacific City), Boiler Bay Research Reserve (Depoe Bay), Pirate Cove Research Reserve (near Depoe Bay), Whale Cove Habitat Refuge (near Depoe Bay), Otter Rock Marine Garden (Devil's Punchbowl), Yaquina Head Marine Garden (north of Newport), Yachats Marine Garden (south of Yachats), Neptune State Park Research Reserve (north of Florence), Gregory Point Research Reserve (Charleston/Coos Bay), Harris Beach Marine Garden (Brookings), and Brookings Research Reserve (Brookings) (Mackey 2006). The Oregon Parks and Recreation Department (ORPD) requires a scientific research permit for all activities that involve specimen collection or fieldwork or that have the potential to damage the natural resources on lands owned and managed by the DSL (Mackey 2006).

As of April 2006, there were no current or pending commercial leases through the DSL for harvest of kelp in submerged lands in Oregon. There was a single active lease for kelp harvest in the intertidal zone of southern Oregon, but this permit was set to expire in mid-2006, and associated harvest should not have involved *Nereocystis*. The levels of personal harvest of kelp in both intertidal and subtidal regions in Oregon have not been quantified and are believed to be low (Mackey 2006).

Washington

History of harvest No evidence of attempts to commercially harvest *Nereocystis* in Washington State could be located.

Historical and current stock assessment Members of the Nearshore Habitat Program of the Washington Department of Natural Resources (DNR) have used aerial photographs to monitor kelp beds fringing the Olympic Peninsula since 1989. The annual surveys are designed to track changes in the size and shape of beds as well as the relative abundance of the two dominant canopy-forming species, *Macrocystis* and *Nereocystis*. The kelp canopy-monitoring study area includes the mainland coastline along the Strait of Juan de Fuca as well as the outer coast of Washington from Port

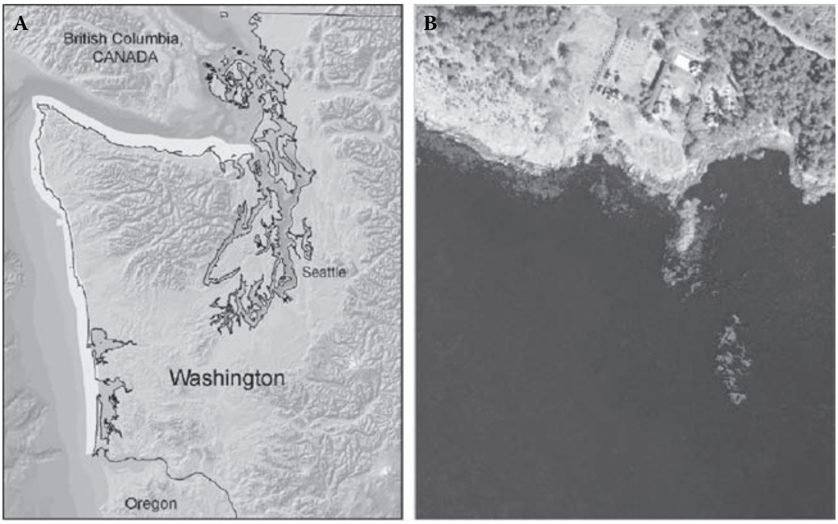

Figure 5 (See also Colour Figure 5 in the insert.) (A) Study area for long-term monitoring of canopy-forming kelp in Washington State conducted by the Department of Natural Resources. (B) Colour-infrared imagery collected by areal surveys. Floating kelp canopies appear as red areas on the dark water surface. Photo interpretation is used to classify red floating kelp as canopy area. Bed area is delineated by grouping classified kelp canopies with a distance threshold of 25 m. (Courtesy of Helen D. Berry, Nearshore Habitat Program, Washington State Department of Natural Resources.)

Townsend to the Columbia River (~360 km of total shoreline; Figure 5A) (Berry et al. 2001). Data are collected according to the following protocol: First, color-infrared photographs of the survey areas, taken at a scale of 1 in:2500 ft, are collected from a fixed-wing aircraft using a 70-mm camera (Figure 5B). The annual inventory is completed in late summer to coincide with the maximum kelp canopy (most often in September). Target conditions for photographic survey days are tidal levels less than +1.0 MLLW (mean low low water), surface winds less than 10 knots, sea/swell less than 5 ft, sun angle greater than 30° from vertical, cloud and fog-free skies. Work evaluating this photo-based assessment technique, conducted in *Nereocystis* beds adjacent to San Juan Island, Washington, demonstrated the potential for tidal height and currents to significantly affect estimates of bed size based on canopy area (Britton-Simmons et al. 2008). Beds appear relatively smaller as current velocity and tidal height increases because subducted plants are more difficult or impossible to detect by aerial photos and near-infrared (NIR) imaging.

Analyses of data collected between 1989 and 2000 revealed pronounced interannual variability in total aerial extent of kelp beds with no consistent long-term trend. Relative to *Macrocystis*, *Nereocystis* beds almost always covered a larger area, were less dense, and exhibited greater interannual variability in their extent. *Nereocystis* also may be more sensitive to climatic anomalies; during the 1997 El Niño, *Nereocystis* populations along the outer coast experienced a 75% reduction in size compared with an 8% reduction for *Macrocystis* (Berry et al. 2001). It has been proposed that reductions in sea urchin abundance and associated kelp grazing, due both to increases in sea otter abundance and direct harvesting of grazer species by humans, may contribute to spatiotemporal variability in the size of kelp beds in Washington. Rigorous quantitative tests of these conjectures have not been performed.

Management and recent harvest Commercial harvest of seaweed, including collection on privately owned tidelands (60% of Washington's intertidal zones), is prohibited except with the approval of both the Washington DNR and the Department of Fish and Wildlife. In 1993, the Washington legislature identified marine aquatic plants as a source of 'essential habitat' in light of their biological importance and economic value and urged the implementation of stricter harvesting regulations (Mackey 2006). At present, seaweeds are only harvested for recreational purposes in Washington (Mackey 2006). Harvesters must be over 15 years of age and can collect no more than 10 pounds of algae (wet weight) per person per day. For *Nereocystis*, fronds are to be cut no closer than 24 in. above the pneumatocyst using a knife or similar instrument (Hillmann 2005). There are three types of non-scientific collection permits in Washington: (1) annual combination permits allow for harvest of seaweed, shellfish, and both fresh and saltwater fishes; (2) annual shellfish and seaweed permits allow for harvest of seaweed and shellfish; and (3) 1- to 5-day combination permits allow the same harvest as the annual combination permits but are valid for no more than 5 days. As of November 2005, the numbers of active permits of these types were 165,983, 161,550, and 196,280, respectively. All but three state parks are closed to seaweed harvesting, and scientific permits, granted only when the proposed collecting has a demonstrable scientific purpose, are required in these parks (Mackey 2006).

In an attempt to conserve nearshore subtidal ecosystems, the Washington DNR has introduced legislation that would authorize the leasing of "submerged lands" for restoration and conservation purposes. Leasing would effectively place these lands, which could include kelp beds, under the stewardship of conservation-oriented individuals or agencies, further protecting coastal environments from commercial harvesting (Mackey 2006).

British Columbia

History of harvest The first attempt at commercial harvesting of marine plants in British Columbia was undertaken by Canada Kelp Company Limited in 1949. Financial complications led to the failure of this endeavour, and no further harvesting operations were initiated until 1967, when nearly the entire coastline of British Columbia was subdivided into 44 harvesting licenses collectively granted to six companies. Two of these never initiated development of their operations, and the remaining four (Sidney Seaweed Products, North Pacific Marine Products [bought out by Kelpac Industries], Pacific Kelp Co., and Intertidal Industries) either failed to reach the harvesting phase or experienced financial difficulties and were operational only briefly. The one exception was Sidney Seaweed Products, a manufacturer of algae-based agricultural products that experienced small-scale economic success from 1965 to 1974. In 1981, the provincial government, through solicitation of harvesting proposals by the Marine Resources Branch of the Ministry of the Environment, adopted a more active approach to establishing a commercial kelp-harvesting industry in British Columbia. Of the applicants, Enmar Resources Corporation was selected and awarded a 5-yr license to operate off the coast of Porcher Island. Despite the support of provincial authorities, the company was ultimately unwilling to initiate development because of a refusal by the federal government of Canada to approve the project. Since that time, harvesting has been confined to small-scale operations collecting a total of less than 100 t yr^{-1} (from Wheeler 1990, Malloch 2000).

Historical and current stock assessment To gather baseline information on spatiotemporal variability in marine plant populations, the Ministry of Fisheries initiated a kelp inventory program in 1975. Surveys are based on the Kelp Inventory Method (KIM-1) developed by Foreman (1975) that uses aerial photographs to estimate the area, density, and species composition of kelp beds. These data are combined with field-collected density and plant weight information to derive biomass estimates for 1-km wide sections of surveyed coastline. By 2000, there were 12 surveys completed, covering the majority of kelp beds that could support large-scale harvesting. Approximately 94% of the standing stock in these beds consisted of *Nereocystis*. As part of a study at Malcom Island, Foreman (1984) concluded that KIM-1 estimates were generally proportional to standing crop values but tended to overestimate these values by approximately 30%. More detailed descriptions of the survey methodology can be found in Foreman (1975) and Wheeler (1990).

Management and Recent Harvest While the responsibility to manage marine plants is assigned to the federal government of Canada by sections 44–47 of the Federal Fisheries Act, a 1976 agreement between national and provincial governments transferred authority to adopt and enforce management regulations to the Ministry of Agriculture, Food, and Fisheries (MAFF) in British Columbia. Licensing applications for commercial harvesting of kelp must still be reviewed by the national-level Department of Fisheries and Oceans (Malloch 2000). The minister has the authority to decline to issue a license if proposed harvesting (1) tends to impair or destroy any bed or part of a bed on which kelp or other aquatic plants grow, (2) tends to impair or destroy the supply of any food for fish, or (3) is detrimental to fish life. Section 35(1) of the Federal Fisheries Act states that no person shall carry on any work or undertaking that results in the harmful alteration, disruption, or destruction of fish habitat. For a permit request to be granted, the applicant must present evidence that the overall operation is economically feasible and that the raw material requirement is low in absolute terms or compared with the estimated standing crop in the desired area or both. Licensing is to be preceded by a stock assessment regardless of the harvest quota requested. If data are not available, a license may be issued with the view to gathering management-related data concurrently with the commercial operation (Wheeler 1990). Licenses are granted annually and issued on a first-come, first-served basis. In an attempt to promote sustainable use of the resource, exclusive access to defined geographic areas is awarded, and harvesters are given the right of first refusal for their assigned localities during licensing renewal reviews (Malloch 2000).

A license costing $110 annually is required only for commercial harvest of kelp. Only Canadian citizens, members of the Canadian armed forces, and persons who are legal permanent residents of Canada are eligible to apply for a license. No more than 20% of the total biomass of a marine plant bed may be harvested, and a royalty of between $10 and $100 per wet ton of tissue is to be paid to the federal government (amounts vary by species). For *Nereocystis*, blades may be cut no closer than 20 cm from the pneumatocyst, and no harvest of the bulb or stipe is permitted. There are no permits required for personal, non-commercial harvest, and collection is prohibited in specially managed areas such as ecological and marine reserves and provincial and federal parks (Hillmann 2005).

Between 1992 and 2000, the number of companies or individuals licensed to commercially harvest marine plants in British Columbia never exceeded 15 (excluding licenses for *Macrocystis* harvesting as part of the herring SOK industry). Non-commercial harvesting is unregulated, and this poses a problem for enforcement of management regulations because the intended use of harvested materials is not always clear. The government of British Columbia has taken steps to incorporate use of marine plants by native/aboriginal groups (First Nations) into the evaluation process for commercial harvesting licenses (Malloch 2000).

Alaska

History of harvest No information on historical harvesting of *Nereocystis* in Alaska could be located.

Historical and current stock assessment The only comprehensive assessment of canopy-forming kelp in Alaska was the ‘potash from kelp’ survey carried out by the U.S. Department of Agriculture (USDA) in 1913. In south-eastern Alaska, 1133 beds, with an estimated area of 18,300 ha and biomass of 7.15×10^6 metric tonnes (mt), were counted. Of these beds, 87% consisted principally of *Nereocystis*, 6% of *Macrocystis*, and 7% of *Eualaria fistulosa*. In the northern Gulf of Alaska, 358 beds, representing an estimated 4610 ha and 3.26×10^6 mt, were recorded. Here, *Nereocystis* made up approximately 55% of the beds, with the remaining 45% being *Eualaria fistulosa* (Frye 1915, Rigg 1915). Based on the results of more recent small-scale surveys, it has been suggested that these values overestimated actual abundance by approximately 10% (Frye 1915, Rigg 1915). The Alaska Department of Fish and Game (ADFG) carries out kelp surveys in conjunction with the commercial herring harvest and the SOK industry, but these rarely involve *Nereocystis* because herring will not spawn on *Nereocystis* (M. Stekoll personal communication). In addition, Alaska

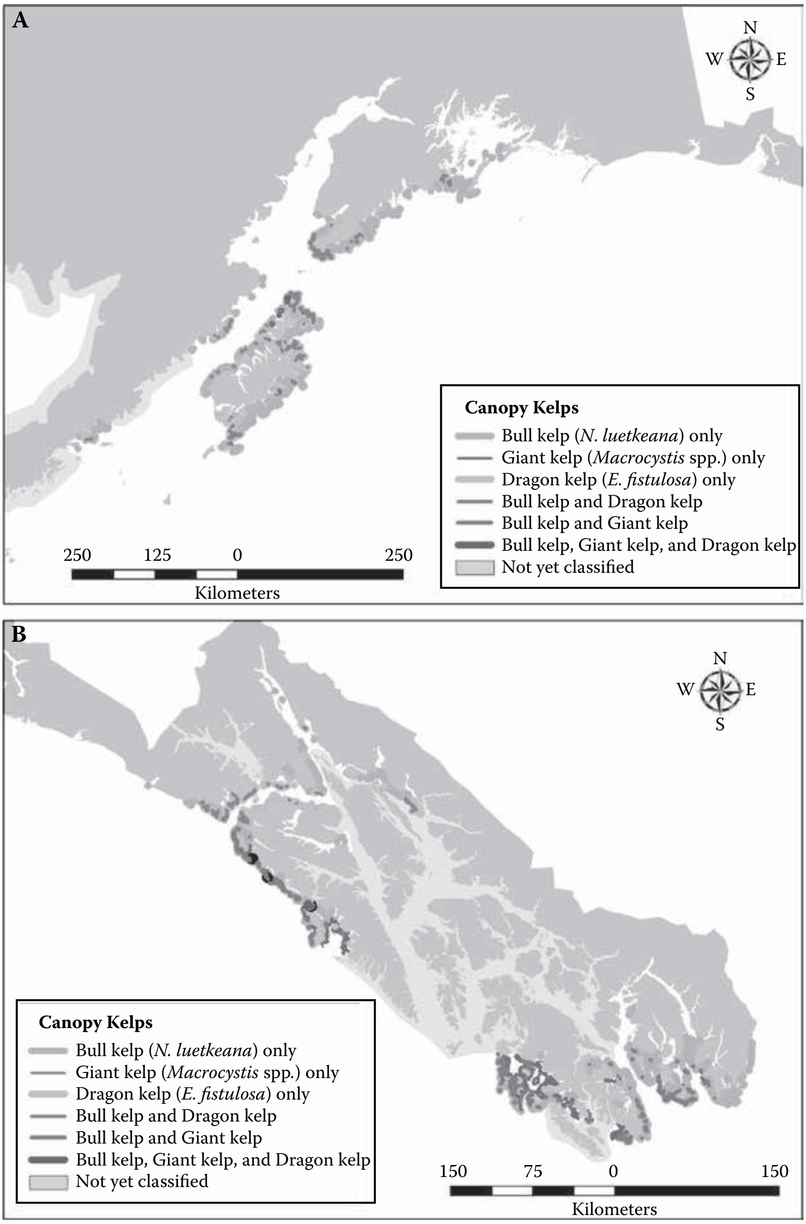

Figure 6 (See also Colour Figure 6 in the insert.) Canopy kelp distribution of *Nereocystis luetkeana*, *Macrocystis* spp., and *Eualaria fistulosa* in (A) Gulf of Alaska and (B) south-east Alaska. (Courtesy Alaska ShoreZone. Program materials available at http://alaskafisheries.noaa.gov/habitat/shorezone/szintro.htm)

ShoreZone, a multiagency coastal mapping program, collects a variety of high-resolution biophysical data from aerial imagery, including the geographic distribution of each of canopy-forming kelp species (Figure 6). Imagery from over 44,000 km of coastline in central and south-eastern Alaska has been recorded, and data from the majority of this region have been mapped and are available through an interactive Web site (http://alaskafisheries.noaa.gov/habitat/shorezone/szintro.htm). The development of an aerial digital multispectral camera (DMSC) imaging system to more accurately and precisely estimate the area and biomass of *Nereocystis* beds in south-eastern Alaska is currently being investigated (Stekoll et al. 2006). Compared with traditional methods of assessment based on aerial photos and NIR imagery, this technology has the advantage of being able to detect submerged plants up to 3 m below the surface of the water.

Management and recent harvest Intertidal and submerged lands in Alaska, from the mean high-tide line out to 3 geographic miles, are owned by the state, and enforcement of harvest regulations is the responsibility of ADFG. Commercial permits are issued by ADFG and required for all commercial harvest. Local ADFG offices decide on the harvest guidelines for their area (M. Stekoll personal communication). Harvesters must report daily records of collection amounts and locations to ADFG once a year. Harvest must be by hand or mechanical cutting and cannot be performed using diving equipment. There are no fees associated with the permit. Collection of *Macrocystis* for herring SOK is subject to different regulations (Hansen & Mumford 1995, Hillmann 2005). A sportfishing license is required for personal collection ($15 annually for Alaska residents, $100 annually for non-residents, no charge for collectors under 16 or over 60 years of age) (Hillmann 2005), but there are apparently no restrictions on take with the exception of the SOK industry (Hansen & Mumford 1995). Scientific permits are available at no cost and require the submission of an annual report of take (number of each species collected, date and location of collection, location of specimen deposition) and of scientific findings associated with the collection (Hansen & Mumford 1995, Hillmann 2005).

Simple Pleasures of Alaska, a small commercial operation out of Sitka, processes *Nereocystis* for making pickles and relish. They harvest approximately 1 t yr^{-1} (B. Pierce personal communication). The Alaska Kelp Company (formerly Pacific Mariculture Company Inc.) of Point Baker, Alaska, was issued a *Nereocystis* harvest permit from the Petersburg ADFG office for 200,000 pounds yr^{-1}. This amount was reduced to 51,000 pounds a few years ago. The Alaska Kelp Company has made a plant fertilizer enhancer from the *Nereocystis,* and it is sold under the names Opticrop, Garden Grog, and Alaska Kelp. One year, they sold about 10,000 t to a company trying to make potting soil from sawdust, fish wastes, and kelp, but it is unclear whether commercial production of the agricultural product was ever initiated (M. Stekoll personal communication).

Pollution

Thermal pollution

Increases in ambient water temperature associated with anthropogenic point-source discharge can cause adverse effects on both gametophytes and young sporophytes of *Nereocystis.* As part of mediation associated with the Diablo Canyon power plant, TERA Corporation (now Tenera Environmental Inc., San Louis Obispo, CA) conducted temperature sensitivity experiments using *Nereocystis* in 1982 (TERA Corporation 1982). Under laboratory conditions, juvenile sporophytes were exposed to water temperatures ranging from 10°C to 20°C for 44 days. The results indicated that prolonged exposure to water temperatures above 18°C is lethal. Furthermore, 25% of the plants held at 15.9°C died after 36 days. A primary cause of mortality appeared to be a reduction in the healing ability of damaged tissue. In the field, Pacific Gas and Electric (PG&E), which operates the plant, noted that in 1985 and 1986 *Nereocystis* plants that came in contact with the thermal discharge plume of the power plant experienced premature blade loss, and *Macrocystis*, a more heat-tolerant species, eventually colonized those sites. *Nereocystis* beds persisted in areas where the thermal plume was deflected (e.g., Diablo Rock) or where cold water conditions were more common due to prevailing currents (discussed in Collins et al. 2000a). These observations were supported by a comparative study performed by Schiel et al. (2004), who used data from an 18-year intertidal and subtidal monitoring program and before-after control-impact (BACI) analyses to demonstrate quantitatively that *Nereocystis* density and abundance were significantly reduced by a 3.5°C rise in water temperature associated with thermal discharge from the Diablo Canyon plant.

Sediment and nutrient run-off (sewage, agriculture, development, dredging, freshwater intrusion)

For *Nereocystis*, the availability of light is perhaps the factor most critical for the growth and sexual maturation of gametophytes and the growth of sporophytes (see population ecology discussion here and discussion in Collins et al. 2000a). Reductions in light penetration could result from a number of processes that increase water turbidity. Sewage discharge and nutrient run-off associated with agriculture could trigger phytoplankton blooms that significantly reduce water clarity. Particulate run-off from the terrestrial environment or the suspension of benthic sediments by dredging activity or storm-associated surge could similarly reduce light penetration. Finally, growth of other algal species near the substratum could overshadow and thereby reduce the germination and growth of gametophytes and young sporophytes. Studies of the effects of sedimentation in nearshore waters have documented reduced *Nereocystis* density in areas associated with landslides (Shaffer & Parks 1994, Konar & Roberts 1996). Burge & Schultz (1973) observed an increase in water turbidity in Diablo Cove, California, following exceptionally heavy rains and associated run-off during the winter of 1968–1969. *Nereocystis* sporophytes were not seen in the area again until mid-July 1969, and the re-emerging bed was reported to be one-quarter the size of the bed in 1968. This reduction in *Nereocystis* abundance was attributed to changes in nearshore light levels (discussed in Collins et al. 2000a), but the large pulse of freshwater run-off associated with this event may have also contributed to the *Nereocystis* dieback. Brown (1915) found that exposure to freshwater for periods of up to a week could cause tissue deterioration. Additional work by Hurd (1916) substantiated this finding, showing that *Nereocystis* sporophytes develop blisters and wilt when subjected to rapid reductions in environmental salinity.

Toxic chemicals

Very little is known about the effects of toxic chemicals on *Nereocystis*. James et al. (1987) showed that, of 10 species of brown algae examined, gametophytes of *Nereocystis* were most sensitive to hydrazine, a chemical used to decrease corrosion in high-pressure boilers. At levels of 0.025 ppm, gametophyte development was inhibited, and sporophyte production would not occur (discussed in Collins et al. 2000a). Antrim et al. (1995), in tests of the effects of diesel fuel, intermediate fuel oil (IFO), and crude oil on *Nereocystis* plants, verified that exposure to petroleum products has a negative effect on *Nereocystis*. Severe tissue necrosis occurred at meristematic tissue between the stipe and bulb. In contrast to these results, comparisons of *Nereocystis* biomass and percentage cover between oiled and control sites in Prince William Sound, Alaska, following the EXXON VALDEZ oil spill, did not indicate any effects of petroleum exposure. *Nereocystis* individuals at oiled sites tended to be smaller, but it was not clear whether this was due to chemical toxicity or preexisting differences arising from natural factors such as recent recruitment or slow growth (discussed in Collins et al. 2000a).

Human modification of species interactions

Human introduction of non-native species into kelp forest ecosystems has the potential to modify species interactions in ways that affect the distribution and abundance of *Nereocystis*. The invasive macroalga *Sargassum muticum* is an example. Introduced to Puget Sound from Japan in the 1940s (Giver 1999), this species occupies space in shallow areas of *Nereocystis* beds and has been shown to competitively exclude *Nereocystis* from these locations under some circumstances (Thom & Hallum 1990). *Sargassum muticum* distribution and abundance is limited to areas associated with lower wave energy, so this type of competitive exclusion is likely to be less common at exposed sites (O'Clair & Lindstron 2000).

More important to *Nereocystis* distribution and abundance than introduced species are natural or human-induced changes in the abundance of species native to kelp forest ecosystems. Central among these are red and purple sea urchins (*Strongylocentrotrus franciscanus* and *S. purpuratus*, respectively) and red abalone (*Haliotis rufescens*; see population ecology section), all species that are currently harvested and fluctuate in density in response to sea otter population dynamics (Vanblaricom & Estes 1988). Native or naturalized epiphytes growing on *Nereocystis* can have a negative impact on kelp growth and survival (see population ecology section and references therein); such epiphyte effects could be particularly pronounced in areas where elevated nutrient concentrations promote growth of epiphytic algae.

Climate change

Episodic El Niños: temperature changes and storms

The reduction in upwelling and increased frequency of severe storms and strong wave action associated with El Niños could all have negative impacts on the distribution and abundance of *Nereocystis*. Suppression of upwelling reduces the amount of cold, nutrient-rich water brought into shallow subtidal areas from depth (Collins et al. 2000a) and can lead to warming of surface waters by up to 4°C for extended periods (McPhaden 1999). As mentioned, *Nereocystis* is sensitive to increases in water temperature, and the availability of nutrients, particularly nitrogen in the form of nitrate, is perhaps second in importance only to light availability as a necessary condition for the growth and reproductive maturation of *Nereocystis*. Perturbations in the physical environment associated with El Niño events thus have the potential to drive reductions in *Nereocystis* abundance and recruitment on interannual timescales. Delayed recruitment and reduced growth of *Nereocystis* in the beds near Fort Bragg, California, in 1992 may have been associated with the El Niño of that year (Kalvass et al. 2001). During the 1997 El Niño, total kelp canopy in Washington decreased by 32%. *Nereocystis* populations along the outer coast were reduced by 75% (compared with only 8% reductions for *Macrocystis*).

While mortality associated with strong storm events and wave action has the potential to reduce the size of *Nereocystis* beds, the ability of *Nereocystis* to rapidly recolonize disturbed areas following the removal of more competitively dominant species of algae such as *Macrocystis* may often accelerate postdisturbance recovery. In 1998, following the reductions in *Nereocystis* abundance in Washington mentioned above, *Nereocystis* populations rebounded dramatically, increasing by 423% (Berry et al. 2001). This dramatic population growth may be evidence of a positive effect of storms on *Nereocystis* abundance arising from temporary release from competition with other algal species for light, nutrients, or primary space. The timing and intensity of storms and the identity and abundance of competing species of sympatric algae are probably important in determining the nature of storm and wave disturbance on *Nereocystis*.

Long-term global warming impacts

Because of its sensitivity to water temperature and preference for cold conditions, *Nereocystis* would likely be adversely affected by increases in sea surface temperature associated with global warming. No data to quantitatively substantiate this speculation are available. Changes in the carbon dioxide concentrations of nearshore waters could offset this impact to some extent. Because global warming is driven to a large extent by increases in atmospheric concentrations of carbon dioxide, it is thought that increased sequestration of carbon dioxide in nearshore marine environments could influence growth rates of photosynthetic organisms. One short-term study showed that doubling ambient carbon dioxide concentrations for 2 h increased the net apparent photosynthetic rate of *Nereocystis* by a factor of between 2.2 and 2.8 (Thom 1996). Temperature-related increases in *Nereocystis* mortality could thus be offset to some extent by enhanced growth under conditions of greater carbon dioxide availability. Swanson & Fox (2007) used a laboratory experiment to test the effects of predicted increases in carbon dioxide and ultraviolet B (UVB) levels on *Nereocystis* development and biochemistry and on grazing by herbivores. Carbon dioxide enrichment increased kelp growth by over threefold, an effect that ameliorated the negative influence of elevated UVB on the same parameter. While tissue phlorotannin (phenolic) concentrations increased as a result of experimental treatments, rates of herbivory by the gastropod *Tegula funebralis* did not differ significantly between experimental and control groups. Results showing slower rates of tissue decay under high carbon dioxide conditions suggest that predicted global climate change could slow rates of nutrient recycling and the export of kelp-associated resources into detritus-based ecosystems.

Incidental damage

Commercial fishing activities can cause direct physical damage to kelp via propeller cuts to blades and stipes. This occurs as boats travel through kelp beds and during the process of 'backing down' when engines are run in reverse to dislodge propellers fouled by kelp fronds and stipes (Collins et al. 2000b). In addition, the deployment and retrieval of fishing gear, particularly crab, lobster, and live fish traps, can cause breakage of fronds and stipes and have the potential to dislodge kelp plant holdfasts from the substratum. Similar effects can be produced during the retrieval of anchors. While deleterious effects on kelp arising from these activities can be appreciable in locations where commercial fishing activity is high or chronic, the extent of kelp damage due to boats and fishing gear is thought to be minimal (Collins et al. 2000b).

Recommendations for management and research to inform management decisions

Overview and challenges for managing the harvest of nereocystis

In contrast to *Macrocystis*, the relatively limited commercial utility and financial value of *Nereocystis* tissue has resulted in minimal attention being paid to the development and implementation of stock assessment programs, harvest record databases, and management guidelines for *Nereocystis*. To some extent, this neglect is understandable because harvest pressure on *Nereocystis* to date appears to be negligible. Across the biogeographic range of *Nereocystis*, commercial harvesting has been confined to a small number of short-lived operations that collected relatively little kelp when compared with the harvesting of *Macrocystis*. There appear to be fewer than 20 active permits for the collection of *Nereocystis* across range of the entire species. No quantitative records of personal (non-commercial) take could be found, but given the relative inaccessibility of subtidal algae this amount is probably minimal.

Management regulations vary widely and appear to be consistent only in the fact that they are based on little if any scientific data on either natural fluctuations in the abundance of *Nereocystis* or effects of harvesting on the demography of *Nereocystis* populations. Aside from recent but spatio-temporally localized surveys conducted by a handful of harvesters and periodic aerial inventories taken by state management agencies, current estimates of *Nereocystis* abundance in many areas of its range may still be based in large part on the results of one or a few comprehensive surveys conducted almost 100 years ago. In contrast to the growing body of literature focused on harvesting impacts on giant kelp populations, only three studies that directly examined the effects of harvesting on *Nereocystis* growth, reproduction, or population dynamics were found. Two of these studies involved such limited replication that the results cannot reasonably be used to inform sound management policies. In addition, because of the fundamental life-history differences between *Macrocystis* and *Nereocystis,* it would be expected that the demographic impacts of harvesting on these two species are fundamentally different, and the extent to which our understanding of *Macrocystis* can be used to create sound policies for the harvest of *Nereocystis* needs to be questioned.

The exceedingly superficial understanding of *Nereocystis* demography and the effects of harvest may be a principle cause of the dramatic variation in *Nereocystis* management regulations in the different political provinces where the species is found. In northern California, commercial harvesting in the 300-series beds that consisted mostly of *Nereocystis* is forbidden or severely restricted. North of the border in Oregon, commercial harvest of kelp and other seaweed has recently been administratively prohibited, although personal collection of up to 2000 pounds of tissue does not require a permit and is largely unmonitored. Further north, Washington State has arguably the most conservative and scientifically sound management policies (Berry et al. 2001, 2005). Surveys of kelp abundance along the shores of the Olympic peninsula, conducted annually since 1989 by members of the Nearshore Habitat Program, provide the only recent, broad-scale, high-resolution, quantitative characterization of the population dynamics of *Nereocystis*. In spite of these relatively detailed stock assessments, the state of Washington prohibits the commercial harvest of *Nereocystis* and limits personal take to 10 pounds permit^{-1} day^{-1}. Unlike all other states and provinces where *Nereocystis* is found, the commercial leasing of subtidal lands and associated kelp beds that often serves as the basis for establishing the boundaries of kelp-harvesting operations is not permitted in Washington. In British Columbia, approximately a dozen stock assessment surveys have been conducted since the 1970s, but most of these were limited in their geographic breadth and did not involve the resampling that is necessary to estimate long-term patterns of kelp abundance at particular localities. The leasing of kelp beds is permitted, but leases must be reapproved each year, and take is limited to less than 20% of the total bed biomass. While coarsely defined permitting regulations are in place in Alaska, we found it exceedingly difficult to collect any information on the number of permits issued and estimates of algal biomass collected by harvesters.

The variability in management regulations is probably evidence of two factors that must be addressed for scientifically sound management policies to be enacted. First, more basic research needs to be done to characterize natural demographic dynamics of *Nereocystis* beds and quantify the effects of harvesting on these dynamics. Data generated by more regular and comprehensive stock assessment surveys can be used by governmental agencies to produce an allocation plan based on accurate knowledge of the kelp resource base and to identify harvestable areas and associated quotas. Commercial operations can also use these data to select locations and capacity requirement of their facilities. Studies of the impacts of harvesting on *Nereocystis* physiology, growth, and demography are critical for the development of management policies that will sustain both the profitability of commercial harvesting operations and the fundamental ecological patterns and process associated with *Nereocystis* beds. Second, greater methodological and legislative consistency among management entities is essential for the type of broad-scale, ecosystem-based approach needed to manage highly interconnected marine populations. Because replenishment of local populations of marine organisms is often a function of both local reproductive output and input from more distant sites, policy makers must look beyond political boundaries to develop biologically comprehensive management strategies. Stock assessment would be greatly facilitated if regulatory agencies from different states could collectively design a survey approach and agree to implement it on a more regular basis. Exchange of data generated by these surveys could be used to develop harvest regulations in a similar consensus-based manner. The use of a common approach to regulate and monitor the impacts of harvesting will facilitate (1) comparison of data from different geographic regions since information is collected using the same methods, (2) maintenance of more comprehensive and intelligible databases on stock assessments and harvest levels, and (3) enforcement of harvest regulations since broadly adopted policies reduce uncertainty about local regulations for both collectors and enforcement agents.

The importance of the lack of biological, economic, and management information for *Nereocystis*, as summarized, is underscored by the strong management implications of many life-history, morphological, physiological, and ecological characteristics of this species (Table 2). It is clear that any ecosystem-based approach to management practices for this and other macroalgae in coastal marine ecosystems will benefit from a strong understanding of the diversity of traits that define a species.

Research recommendations

The synthesis of the literature presented generated a series of recommendations for future research that could substantially improve our ability to manage human impacts on *Nereocystis*. These recommendations include studies designed to better our knowledge of (1) the status, dynamics, and use of *Nereocystis* populations; (2) impacts of harvest on the sustainability (resilience and replenishment) of *Nereocystis* populations; (3) impacts of harvest of *Nereocystis* on shallow reef ecosystems; and (4) impacts of harvest on other coastal marine ecosystems. These recommendations are listed in the order that we believe they should be prioritized.

Stock and resource assessment methodologies

Central to any resource management programme is knowledge of the status, dynamics, and use of the resource. Like *Macrocystis* stock assessments, aerial digital image-based measures of canopy cover appear to be the most cost-effective method for assessing kelp abundance and distribution, although multispectral imaging techniques show promise (Stekoll et al. 2006). However, the accuracy and precision of these traditional methods are questionable (e.g., Schiel et al. 2004), and variation in potentially confounding factors (e.g., tides, currents, sea conditions, atmospheric conditions, timing) must be more closely examined. Surveys to test the functional relationship between diver-based estimates of plant density and biomass and estimates of abundance from aerial surveys or images would provide ground-truthing of the aerial-based estimates and perhaps allow translation of canopy cover to biomass estimates. Thus, a well designed study of the use of aerial digital imagery is recommended as a foundation for a more comprehensive stock assessment. Like other recommendations that follow, and as mentioned in the preceding section, such efforts should be coordinated across states to ensure consistency in stock assessments over the range of the species.

Potential impacts of harvest on the resources

Relative impacts of different harvest methods The commercial and recreational harvest of *Nereocystis* includes several variables, the relative ecological impacts of which have not been tested. Such variables include hand versus mechanical harvest; whole-plant versus partial-blade removal; the relative extent (percentage of stand) and location (outer, middle, or inner) of harvest of a bed; and timing of harvest relative to plant phenology. For example, is there a threshold percentage of a forest that should not be harvested to ensure local re-establishment? Can the impact of harvest on growth and reproduction of *Nereocystis* be minimized by timing harvest according to plant phenology? Does phenology vary geographically and, if so, in what ways? Because some literature hints at the possibility of spores overwintering (a biennial rather than annual reproductive cycle), further exploration of this possibility should be conducted to determine if generations can overlap. Equally important will be the identification of one or more quantifiable metrics to be used to assess the impacts of different harvesting strategies. These metrics (e.g., abundance of adult plants in the year following harvest) would ideally be (1) directly linked to demographic patterns or rates associated with the *Nereocystis* populations being harvested and (2) easy to measure. Finally, indirect effects of harvesting on the distribution or abundance of adults, manifested via impacts on gametophytes, must be investigated. Because interannual changes in sporophyte abundance are inexorably linked by a gametophyte stage, more information is needed on gametophyte abundance, distribution, and longevity and the

Table 2 Implications of species traits and ecological patterns of bull kelp *Nereocystis luetkeana* for harvest management

Biological trait	Ecological pattern	Implications for harvest management/ ecosystem management
Morphological and physiological traits		
Non-buoyant stipe with pneumatocyst at the surface as sole source of buoyancy.	Loss of pneumatocyst leads to mortality, loss of entire alga.	Unlike giant kelp, surface harvest will cause bull kelp to sink and die; may be vulnerable to epiphyte smothering in nutrient-rich waters.
All reproductive and majority of photosynthetic tissue attached to pneumatocyst at the surface.	Individuals and populations persistent in areas of high turbidity.	Plants highly vulnerable to destructive activities at the surface: harvest, damage from boat props, retrieval of fishing gear and anchors.
High morphological plasticity of blade shape (narrower in high-surge areas).	Reduced productivity in areas of high surge.	Harvest rate may require spatial (habitat-based) regulation to accommodate variation in productivity.
Sensitive to water temperature.	Geographic and latitudinal changes in distribution reported in literature.	Potentially vulnerable to ocean temperature shifts, including frequency and intensity of El Niño; may result in shift to deeper water and constrain and eliminate populations simultaneously limited by light attenuation.
Early life stages (i.e., gametes, spores) sensitive to light availability.	Depending on water clarity, sedimentation, and abundance of competitors (other algae), sporadic reproductive success, high interannual variability.	Germination, growth, and survival, especially of gametophytes and young sporophytes, may be strongly influenced by runoff, sedimentation, eutrophication.
Very high rate of individual growth.	Rapid replenishment of harvested populations.	Proper management practice could maintain high production.
Sperm/egg fertilization pheromone driven.	High population density (close proximity of individuals) critical to success and rate of reproduction; combined with limited propagule dispersal, highly vulnerable to Allee effect and local extinction.	Local harvest rates need to ensure sufficient density and propagule production.
Life-history traits		
Annual life history.	Population dynamics highly variable in space and time; highly seasonal variation in abundance.	Highly sensitive to timing and magnitude of harvest. Vulnerable to local extinction if harvested before reproductive maturity and spore production.
Spore dispersal probably highly limited.	Interannual rates of recolonization highly dependent on rate of local spore production.	Highly sensitive to timing and magnitude of harvest. Vulnerable to local extinction if harvested before reproductive maturity and spore production.
Ecological traits		
Local populations form beds of high plant density.	Dominant or only bed-forming kelp across much of its range.	Provides much of the physical, 3-dimensional structure of shallow rocky reef ecosystem, increasing diversity of physical habitats and potentially altering water flow, which can influence delivery of larvae and nutrients.

Table 2 (continued) Implications of species traits and ecological patterns of bull kelp *Nereocystis luetkeana* for harvest management

Biological trait	Ecological pattern	Implications for harvest management/ ecosystem management
Forms surface canopy.	Predominant or only surface canopy-forming algae throughout much of its geographic range.	Removal of canopy may reduce rates of recruitment and survival of juvenile fishes and invertebrates.
Poor competitor, especially as gametophyte and juvenile sporophyte.	If removal of bull kelp enhances development of understory algae, can reduce regeneration rate.	Slower recovery in response to overharvest.
Strongly impacted by herbivore grazing.	Single stipe that cannot regenerate lends entire alga vulnerable to damage by grazers; grazers can cause both direct damage and indirectly influence growth of gametophytes and young sporophytes by grazing on benthic algae, which compete for light and space.	Management of impacts on herbivore grazers and their predators can have strong direct and indirect effects on bull kelp.
Distribution is largely limited by competition to high-surge environments.	Association with sites of high wave exposure may limit accessibility for harvest.	Harvest may be inaccessible over large portions of the population and disproportionately high at sites with greater accessibility.

sensitivity of these factors to environmental changes that may arise from harvesting of sporophytes (e.g., sedimentation, light and nutrient availability, competition for space with understory algae and invertebrates). The recent development of a molecular technique to detect the microscopic life stages may greatly facilitate the collection of relevant information (Fox & Swanson 2007).

Spatial components of replenishment of harvested populations

Virtually nothing is known about spatial patterns of population connectivity (i.e., the transport of spores from one population to another) in *Nereocystis*. Such information is key to determining the distances over which dispersal from neighbouring kelp forests can be expected to help replenish harvested forests. What is the dispersal kernel for *Nereocystis* spores, and does this vary regionally? This information will help determine the relative vulnerability of forests based in part on their size and isolation. There is evidence that *Macrocystis* spores must settle at a threshold density to ensure successful subsequent fertilization between the male and female gametophytes. At lower densities, gametophytes are separated from one another by too great a distance for successful encounters of eggs and sperm to occur with appreciable frequency. Whether this Allee effect holds true for *Nereocystis* is unknown. If present, it could have profound implications for the level of harvest and remaining density of reproductive plants necessary to ensure replenishment of a forest. In addition to field-based studies of dispersal, analysis of population genetic structure would be instrumental in assessing population connectivity and would be useful in identifying regions with unique genetic composition with an eye toward preserving the genetic diversity of the species at the biogeographic scale.

Potential impact of harvest on kelp forest ecosystems

This review of the literature revealed a startling paucity of research on the role of *Nereocystis* in shallow rocky reef ecosystems. With the exception of a few widely separated studies, few rigorous assessments of the presence or density of *Nereocystis* on the structure and functions of associated algal, invertebrate, or fish assemblages have been made. Because of its ephemeral occurrence and lack of structural complexity, *Nereocystis* may not be nearly as influential as *Macrocystis* on kelp forest communities. However, because it is often the only source of habitat that extends to the water surface in many localities, and juvenile fishes have been observed to strongly associate with the kelp canopy, it may in fact be a particularly important source of habitat. Moreover, because of its rapid growth rate and production of detritus, *Nereocystis* may be an important source of nutrient resources for key species in shallow reef ecosystems (e.g., sea urchins, abalone). Some important questions that remain unanswered include the following: Are there invertebrate or fish species that are strongly influenced by the presence of *Nereocystis* forests, such that harvesting indirectly effects their local and regional distribution and abundance, and how does this vary geographically? What is the competitive relationship between *Nereocystis* and other species such that removal of a forest at a particular time allows competitors to increase and preempt regeneration (as has been observed between *Macrocystis* and *Sargassum* in some regions)? What is the role of *Nereocystis* in the detrital pathway on shallow reefs and the sustainability of other resources (e.g., sea urchins, abalone)? Answers to these questions will require both surveys to examine the generality of relationships and experiments to definitively test for causality in these relationships.

Potential impacts of harvest on other coastal marine ecosystems

Like *Macrocystis*, the great amount of biomass produced by and lost from *Nereocystis* forests each year can be transported to adjacent ecosystems on shore (e.g., sandy beaches, rocky intertidal areas) and off shore (e.g., deep rocky reefs, submarine canyons), where it fuels detritus-based trophic pathways and creates temporary habitat structure. The magnitude and consequence of this connectivity among ecosystems is poorly understood. What is the role of *Nereocystis* in maintaining connectivity between the nearshore kelp forests and other marine ecosystems, and how will reduction of canopy export to these ecosystems influence their structure and functions? Studies designed to survey and manipulate this influx would provide useful insight into the importance of this process.

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