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ECOLOGY and MANAGEMENT of the BULL KELP, *NEREOCYSTIS LUETKEANA:*
A Synthesis with Recommendations for Future Research

By

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Cover: Bull kelp (*Nereocystis luetkeana*) with surf perch. Photo by Steve Clabuesch.

Forward

This report, prepared by Y. Springer, C. Hays, M. Carr and M. Mackey, is the result of a project initiated and supported by the Lenfest Ocean Program. It has been peer reviewed by several experts familiar with kelp ecology.

Additional copies of the report are available at www.lenfestocean.org\publications. A policy-oriented synopsis of these research results is available at www.lenfestocean.org\publications. A scientific summary of the results has been submitted for publication and will be available, when published at www.lenfestocean.org\publications.

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I. Introduction

Why the interest in ecology and management of the bull kelp?

Species of large brown algae of the order Laminariales, referred to as kelps, are a conspicuous component of coastal rocky reef habitats in temperate oceans throughout the world. Along the west 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 (< 30m depth) rocky habitats. Because of their fast growth rate and large stature, these algae are thought to contribute markedly to both the productivity of shallow coastal marine ecosystems and as habitat for a diversity of fishes and invertebrates (Foster and Schiel 1985; Graham 2004; Graham et al. in press). Both of these fundamental ecosystem functions of kelps are realized not only by those species that reside in kelp forests throughout their lives, but also by species that use these habitats as foraging grounds (e.g., shore birds, sea otters), and nurseries (particularly fishes), for the enhanced growth and survival provided them by the productivity and structural refuge created by the algae (see review by Carr and Syms (2006)). Many of these species have been strongly impacted by overfishing and are the focus of conservation efforts (e.g., rockfishes, sea otters). In addition, algae represent important biological links between marine ecosystems. The biomass and nutrients they produce, in the forms of detritus or entire 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 (Harrold et al. 1998; Kim 1992; Vetter 1995). Floating kelp rafts also may serve as habitat for larval and juvenile fishes, effectively transporting them among spatially isolated local populations of adults (Hobday 2000; Kingsford 1992; Kokita and Omori 1998). Because of the ecosystem functions provided by kelps, the consequences of human impacts to these forests are not limited to the direct effects on kelp populations, but influence indirectly the many species that depend on the presence of these forests.

In addition to the functional roles that kelp play in coastal marine ecosystems, they contribute valuable ecosystem services. Not only do they contribute to the productivity of coastal fisheries through the functions they perform for coastal fishes, but the algae themselves are extracted for human consumption, pharmaceutical industries, and as food for the commercial mariculture of abalone. The physical barrier created by forests that line the shore also dampens ocean waves, thereby reducing coastal erosion. They are also of great social and cultural importance because of the myriad of species these forests harbor that foster many human activities (e.g., commercial and recreational fishing, scuba diving, bird watching, kayaking.) Separately, and in combination, these consumptive and non-consumptive activities can translate into socioeconomic values of importance to local coastal communities.

Due to their close proximity to shore, kelp forests are subjected to deleterious anthropogenic impacts that can impair the functions and services they produce. In addition to the direct extraction of kelps, they can be exposed to coastal pollution in the form of nutrient discharge from urban and agricultural sources and thermal pollution from the discharge of cooling waters associated with 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. In addition to

these localized and regional threats, kelp forests are vulnerable to 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 change in response to large-scale climate trends, 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 events are major causes of mortality and the loss of entire kelp forests (Tegner and Dayton 1987). The frequency, duration, and strength of El Niño events have increased in recent years, and these changes may be a direct consequence of concurrent regional climate changes (Trenberth and 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. Large specially designed harvesting vessels were used to remove large swaths across forests. Removal is limited to the upper 2 m of the forest 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 portions of the algae are located at the base of the plant and remain intact during and subsequent to the removal of the canopy. Thus, the algae are able to reproduce and forests persist in the face of large-scale mechanical extraction. However, the indirect effects to the fishes and invertebrates that use the forest canopy as nursery habitat and 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 bull kelp, *Nereocystis luetkeana*, is a more recent development, fueled by the demands of abalone mariculture and human consumption. Though relatively smaller in volume and geographic extent, the harvest of bull kelp is problematic. Extraction is primarily by hand from a boat and, like giant kelp, limited to the upper 2 m of the forest. However, the source of buoyancy that keeps the alga upright, along with the reproductive organs of bull kelp, are located at the top of the alga and are thereby removed when the upper portion of the plant is cut off. Because bull kelp is an annual species, removal of the upper portion of plants prior to reproduction can potentially preclude the production of subsequent generations. Because the spores of bull kelp are thought to move very short distances (10's of meters) on average, local impairment of reproduction might terminate the persistence of a forest. Local recruitment could be subsidize by input of spores from other populations delivered either by drifting reproductive sporophytes or abscised sori. Additionally, the presence of dormant spores produced by previous generations of bull kelp could potentially reseed local populations that have been depleted by harvesting. Because there are few data on spores dispersal potential and dormancy durations, however, these mechanisms of local "rescue" cannot at present be incorporated into management plans in a quantitative manner.

Approach, scope of synthesis, and products

Ecosystem-based management of coastal marine resources is based, in part, on scientific understanding of the broad (i.e. ecosystem-wide) consequences of human uses of the coastal environment, including resource extraction and degradation of habitats. To wisely manage these

resources, a clear understanding of the potential impacts of human activities on the resource and the ecosystem is essential. To contribute to this understanding, this report synthesizes the state of knowledge of (1) the ecology of the bull kelp and its role in coastal ecosystems, (2) the past and present human uses of and impacts on this species and, by extension, the coastal ecosystem, and (3) the past and present approaches to managing this resource. We use this synthesis to identify gaps in our knowledge required to make sound management decisions, and recommend 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 both data published in peer-reviewed, scientific journals and non-peer-reviewed data (e.g., produced by governmental agencies and NGOs).

This report includes three components: the written summary included here, an electronic database of all the material used to generate this synthesis, and a compilation of most of this published and gray literature in the form of PDF documents. The literature database was compiled in EndNote (version X), one of the most popular and readily available electronic bibliographic databases. The collection of PDF documents will be available as linked attachments through the Endnote library file as well as on the web at both Dr. Carr's website at UC Santa Cruz and the Pacific Marine Conservation Council website.

II. REVIEW/SYNTHESIS OF ECOLOGY

Species description and geographic distribution

Nereocystis, or bull kelp, is a conspicuous brown macroalga in the nearshore environment on the Pacific Coast of North America. The blades of the alga (30-60 on an adult sporophyte) 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 substrate with a hapterous holdfast (Figure 1). Up to 1/3 of the upper portion of the stipe is hollow, and the stipe is extremely elastic; exposed to wave force, it can stretch more than 38% (Koehl and Wainwright 1977). Because all of an individual's blades are at or near the water surface, the canopy provides virtually all substrate for photosynthesis and nutrient uptake, and photosynthate is subsequently translocated throughout the rest of the thallus via sieve elements in the medulla (Nicholson 1968; Schmitz and Srivastava 1976).
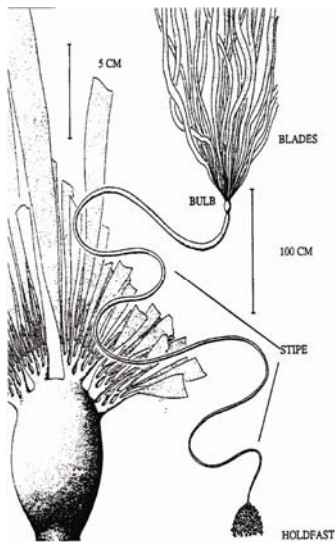

Figure 1. Diagram of bull kelp morphology (Abbott and Hollenberg 1976)

Bull kelp forms extensive beds from Point Conception, CA, to Unmak Island, AK (Abbott and Hollenberg 1976; Miller and Estes 1989), on bedrock, reefs and boulder fields 3 to 20 meters deep (Nicholson 1970; Vadas 1972). *Nereocystis* and *Macrocystis* also form mixed stands in southeast Alaska and British Columbia. Unattached adult plants (i.e. their holdfasts dislodged from the substrate) 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 and Zhigadlova 1997). In the southern portion of the range, south of Ano Nuevo Island (north of Santa Cruz, CA) both bull kelp and giant kelp (*Macrocystis*) occur together, sometimes forming mixed kelp beds; north of Santa Cruz, CA, bull kelp is the dominant canopy-forming kelp (Dayton 1985; Dayton et al. 1984; Foster 1982; Foster and Schiel 1985; Harrold et al. 1998)}.

Evolutionary history

Seaweeds are a polyphyletic group of organisms with very different evolutionary histories. *Nereocystis luetkeana* is a large brown alga (Division Heterokontophyta) in the order Laminariales (the true kelps). There are at least 100 species of kelps worldwide (Guiry et al. 2006), and this group includes other common species such as *Macrocystis* (giant kelp) and *Postelsia* (sea palm). *Nereocystis* is a monotypic genus in the order Laminariales; traditional taxonomy, largely based on sporophyte morphology, places it within the family Lessoniaceae (Setchell and Gardner 1925). With the advent and increasing accessibility of molecular techniques, the evolutionary relationships among kelp taxa, especially among the three 'derived families' (i.e. Alariaceae, Lessoniaceae, and Laminariaceae) has been the topic of increased scrutiny and debate (Coyer et al. 2001; Saunders and Druehl 1991; Saunders and Druehl 1993). The most comprehensive genetic data to date suggest that *Nereocystis* 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 and 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 lab with *Macrocystis* (Lewis and Neushul 1995), in spite of differences in chromosome number (Sanbonsuga and Neushul 1978). However, this is likely to be an artifact of the lab, and reflective of parthenogenesis or male apogamy rather than actual hybridization (Druehl et al. 2005). No hybrids between bull kelp and giant kelp have ever been found in the field.

Life history

Like all kelp species, bull kelp exhibits alternation of generations between a large, diploid sporophyte stage and a microscopic haploid gametophyte stage (see Figure 2). 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 and Foreman 1980). Bull kelp sporophytes can grow at extremely high rates, up to 6 cm per day (Scagel 1947). Maximum photosynthesis occurs in summer and early fall, and mortality of bull kelp sporophytes spikes in the winter, primarily due to being washed out by winter storms. Lower kelp densities after a storm event can also cause surviving individuals to experience increased grazing pressure from 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 bull kelp 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.
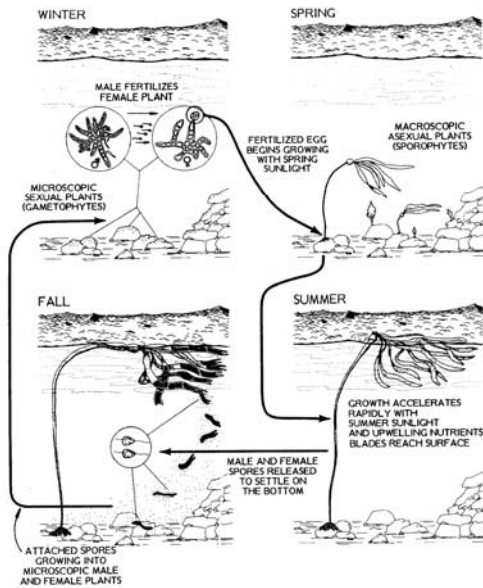
Figure 2. Diagram of bull kelp lifecycle (from report by Tera Corporation (Corporation 1982)

Bull kelp sporophytes produce biflagellate haploid spores through reduction division on fertile patches of blades called sori. Sori may be >30 cm in length, and are produced near the proximal end of the blade (Scagel 1947). Thus patches increase in maturity with increasing distance towards the distal edge (Nicholson 1970; Walker 1980a; Walker and Bisalputra 1975). *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 1-4 hours of abscission, virtually all spores are released from the sorus (Amsler and Neushul 1989; Nicholson 1970; Walker 1980b).

Spores that successfully settle germinate into microscopic sessile gametophytes, which are uniserate branched filaments. Compared to the conspicuous sporophyte stage, little is known about the ecology of kelp gametophytes; for example, it is unclear how long bull kelp 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 2-3 months, exposed to suitable light and nutrients, gametophytes produce oogamous gametes. Vadas (1972) showed that under limited light conditions in the lab, gametophytes may survive and grow vegetatively for over a year before a change in conditions allows the production of gametes. This suggests that bull kelp gametophytes may act in a manner analogous to a terrestrial seed bank (e.g., (Edwards 2000)). Alternatively, seasonality may be imposed by larger-scale phenomena such as strong winter storm events and the abiotic environmental changes that accompany them.
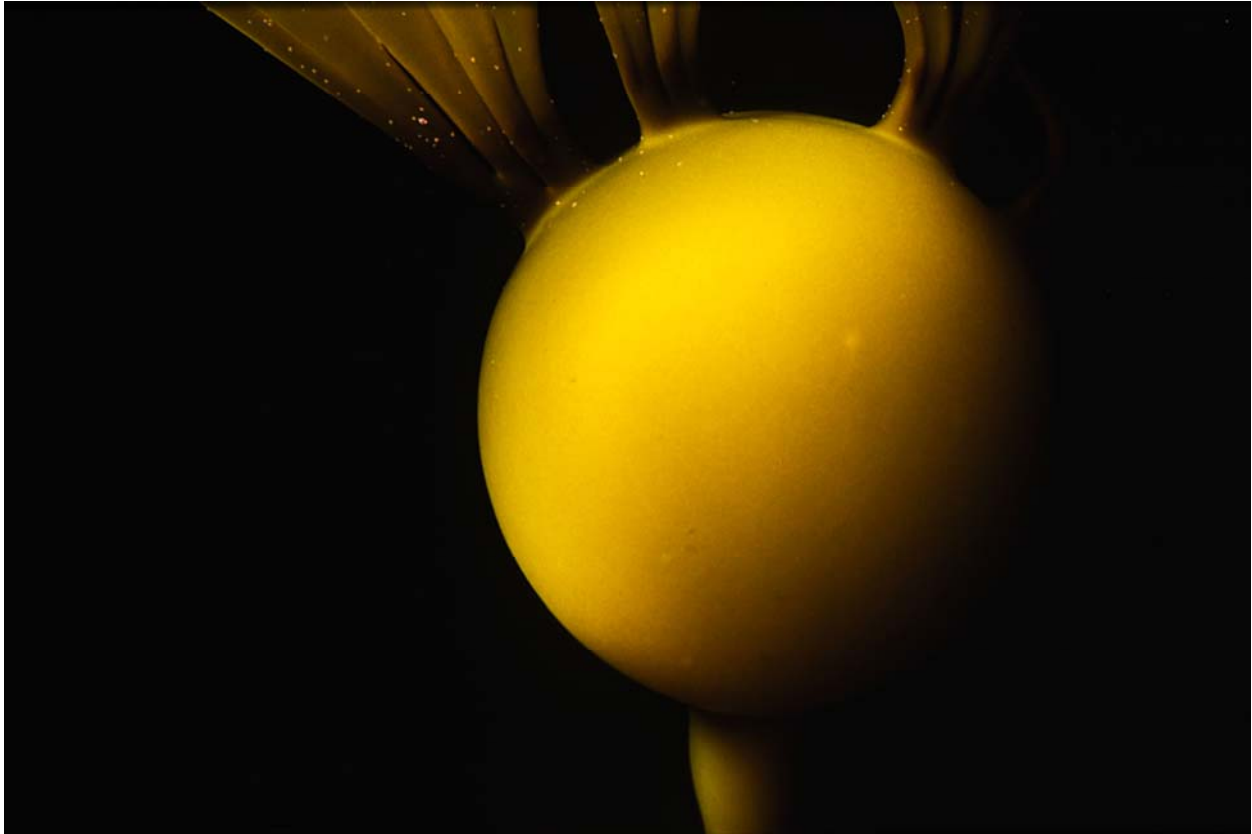
Figure 3. By Jim Patterson © Jim Patterson Photography

Kelp eggs release sexual pheromones that act to attract sperm (Maier et al. 1987); however, the spatial scale over which this mechanism promotes successful syngamy is very low.   Thus the density of settling spores, and resulting proximity of male and female gametophytes, is 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 bull kelp recruitment is not known, but is likely to be similar in scale.

Population Ecology

1. 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; see above) are only effective when gametes are within about 1 mm of each other (Maier and Muller 1986; Muller 1981). Thus there are three possible points in the bull kelp life history where dispersal may occur; as spores, and as intact sporophytes, and as detached sori. Detached sori and intact dislodged sporophytes have the potential for very 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 (estimated mean of 2.3 X 10^5 spores release per cm^2 of sori per min during initial release; (Amsler and Neushul 1989)) and release them at a faster rate than giant kelp (approximately 6x faster; (CEQA 2001a)). Individual plants produce sori on different blades at the same time; thus sori mature and are released somewhat synchronously, in pulses that occur every 4-6 days (Amsler and Neushul 1989). Spore production and release occurs with a monthly and daily periodicity that varies with geographic location. In British Columbia, bull kelp 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 and Neushul 1989). Sori abscission does have a distinct dial pattern in Central California, such that most abscission occurs in the hours immediately before and after dawn (Amsler and Neushul 1989). Like other kelps (e.g., *Macrocystis*, *Laminaria farlowii*), bull kelp spores are capable of photosynthesis; although net photosynthesis is low (Watson and Casper 1984), spores should be able to contribute to their own carbon needs. Thus dawn release may reflect an adaptation to maximize photosynthetic opportunity (e.g., to increase viability in the plankton, or maximize energy reserves for early growth/germination).

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

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

2. Spatial/temporal variation in population dynamics

Nereocystis shows strong spatial and temporal variability in distribution and abundance patterns, consistent with its ruderal and annual life history. For example, in a study of the effects of harvest on bull kelp dynamics, Foreman (1984) found greater interannual variability in abundance in 1-hectare control plots than in plots that had been harvested. See "Historical and Current Stock Assessments" sections below (III. Human Activities and Management: Harvest) for a description of available data on spatial and temporal variation in *Nereocystis* cover/productivity across the species' range.

The reproductive phenology of bull kelp also varies spatially, seemingly with sporophyte recruitment and spore production occurring earlier in more northern populations. Burge and

Schultz (1973) studied *Nereocystis* in Diablo Cove, CA, documenting initiation of new sporophytes from late March through August. Sori were present on blades before they reached the water surface, with complete abscission of sori occurring over a broad window of time: as early as June, and as late as March of the following year. More than 1600 km to the north, in Tacoma Narrows, WA, *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 and Miller 1996). In the westernmost population in the species' current distribution (Umnak Island, AK), Miller and Estes (1989) observed sporophytes in July showing characteristics (i.e. size, maturity, and epiphyte cover) that typically reflect individual condition in fall/winter. There was no evidence of 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, etc.) in Barkley Sound, British Columbia, from June through October, and found that peak fertility occurred in early July, with a smaller peak occurring in September/October. No comparable data on seasonal variation in spore production are available for CA populations (according to (CEQA 2001a).

3. Abiotic and biotic factors limiting distribution and abundance

Physical factors known to influence the distribution and abundance of subtidal kelps species include irradiance, substrata, sedimentation, nutrient levels, temperature, water motion and salinity. As pointed out by Dayton (1985), their effects are often difficult to understand, as 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: Culture studies with bull kelp suggest that the total quantity of light (photoperiod x intensity) is the single most important factor in the development of both gametophytes and young sporophytes (Vadas 1972). Further, the range of conditions under which vegetative growth is maintained is broader than the conditions necessary for reproduction. In the lab culture, gametophytes did not reach sexual maturity under light levels less than 15 foot candles. In mature kelp forests light availability is typically well below this threshold; thus it appears that bull kelp 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 and Freshwater 1988). The decline of bull kelp near warm water discharge from the Diablo Canyon power plant ((PGE 1987); see human impacts) supports this idea. Culture studies with *Nereocystis* show that the thermal conditions allowing sporophyte and gametophyte reproduction range from 3º C to 17º C (Vadas 1972). Much of the Aleutian chain is influenced by the Kuroshio current, so it seems unlikely that thermal constraints alone could drive the sharp northern/western boundary observed at Umnak Island. Instead, Miller and Estes suggest that light limitation driven by the high fog cover characteristic of the western islands, especially in the summer, may act to prevent spread (Miller and Estes 1989).

Nutrient levels: Both spatial and temporal variation in nutrient availability can have a strong influence on kelp productivity (Dawson 1966; Rosell and Srivastava 1984). The seasonal growth pattern of bull kelp 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 bull kelp peak, a shift that typically indicates lower nitrogen availability (Rosell and Srivastava 1985). Like other kelps, *Nereocystis* displays simultaneous uptake of both nitrate and ammonium, but a preference for NO_3^-; Ahn et. al. (1998) found that nitrate uptake by bull kelp increased linearly with nitrate availability, up to the highest concentration tested (30 uM). In contrast, ammonium uptake rates reached a plateau at availabilities greater than 10 uM. In addition to macronutrients and micronutrients known to influence algal productivity in general (e.g., phosphate, potassium, calcium, magnesium), bull kelp also has the capacity to uptake other metallic and non-metallic compounds from seawater (Whyte and Englar 1980a; Whyte and Englar 1980b); 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)).   Bull kelp is relatively resistant to dislodgement compared to other large kelps, and is typically found in nearshore habitats characterized by high wave action. This is especially true in the southern portion of its geographic range, where it overlaps in distribution with giant kelp. In northern part of range, bull kelp survival (and distribution) shows 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 bull kelp stipe/holdfast. This interaction between physical and biotic stresses is thought to be why northern bull kelp populations are seldom found in habitats with intermediate flow energy: the combination of both high grazing pressure and periodic high drag forces exerted on herbivore-damaged kelp results in a sharp increase in sporophyte mortality rate.

Bull kelp is a striking exception to the general rule that wave-swept organisms tend to be smaller than their sister taxa in calmer waters. This observation has intrigued biologists for the past decade, and led to a series of biomechanical studies of bull kelp morphology. For example, see Koehl and Wainwright (1977) and Johnson and Koehl (1994) for a consideration of unidirectional flow, and Denny et al. (1997) for an analysis of dynamic flow effects. Bull kelp also shows dramatic phenotypic plasticity in frond morphology in response to flow. At relatively calm sites, bull kelp produce blades that are wide and undulate with wavy margins; in more exposed habitats, bull kelp produce narrow, strap-like blades. This plasticity in form is thought to arise from a trade off between dislodgement risk and photosynthesis: the narrow blade morph is better able to withstand drag forces experienced on the open coast, but experiences greater self-shading than the individuals with ruffled blades (Koehl and Alberte 1988).

Figure 4. *Nereocystis* blades. Image courtesy of Steve Clabuesch.

Grazers: Major grazers of *Nereocystis* include red and purple sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) and red abalone (*Haliotis rufescens*), as well as limpets (e.g., *Collisella pelta*), snails (e.g., *Tegula* spp, *Callistoma* spp) and crustaceans (Burge and Schultz 1973; Cox 1962; Nicholson 1968). 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., (Duggins 1980; Pace 1981; Paine and Vadas 1969). When urchins are removed from the system, the presence and density of bull kelp sporophytes can increase dramatically. Breen et al. (1976) found that the density and area of *Nereocystis* beds increased following removal of red sea urchins. Kelp density in these beds also increased. In a study by Pace (1981) performed in Barkley Sound, *Nereocystis* density increased from 4.6 plants/m^2 to 13.9 plants/m^2 in a single year following experimental removal of red 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 bull kelp. Increases in the size and density of *Nereocystis* beds near Fort Bragg between 1985 and 1988 were appear to have been correlated with the commercial harvest of roughly 32,500 tons of red sea urchins from areas off the Mendocino and Sonoma counties (Kalvass et al. 2004). Several studies have also demonstrated that the seaward limit of bull kelp beds may be set by urchin grazing (Breen et al. 1976; Pearse and Hines 1979). The species' capacity for rapid growth under high light

conditions permits fast recovery by bull kelp sporophytes when the canopy opens up due to grazing or other disturbance: for example, Foreman (1977a) showed that bull kelp underwent the largest variation in biomass of any algal species over the course of recovery from a grazing event by green urchins in the Strait of Georgia, B.C., and dominated the algal community for a period of more than four years before declining towards pre-disturbance levels.

In addition to direct 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 bull kelp stipe/holdfast, and increase an individual plant's vulnerability to wave action, as discussed above. Koehl and 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 anectodal connection could be found. Herbivory can also alter the competitive hierarchy among kelps and other macroalgae (Paine 2002), and reduction of herbivores may adversely affect *Nereocystis* by increasing competition with other algal species. In the absence of herbivory, species of understory and turf algae such as coralline algae, foliose reds (*Botryoglossum farlowianum, Polyneura latissima*), and midwater canopy species (*Laminaria spp., Pterygophora californica, Eisenis arborea*) can reach high levels of abundance and prevent the recruitment of bull kelp via competition for primary space and overshadowing (discussed in (CEQA 2001b). Such effects have been observed in association with a number of different mechanisms: following mass disease-related mortality of sea urchins in Carmel, CA (Pearse and 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; Estes and Duggins 1995; Gotshall et al. 1984), and the commercial harvest of red sea urchins near Fort Bragg, CA (CEQA 2001b). The beneficial effects of urchin grazing on bull kelp may be particularly important in areas of heavy scour and unstable substrates (Duggins 1980). Thus the net effects of herbivory on bull kelp beds will be driven both by the abundance and feeding preferences of grazers and the nature of competitive interactions between *Nereocystis* and other species of algae that co-occur at a given location. Further, although grazing is clearly an important driver of bull kelp population dynamics, the effects of different grazer species on per capita rates of bull kelp 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 above, competition is another major driver of bull kelp distribution, both within and across sites. *Nereocystis* is generally thought to be opportunistic or ruderal kelp that is usually out competed by perennial species in the absence of disturbance (Dayton 1985; Dayton et al. 1984). (See Figure 5). Where bull and giant kelp co-occur, bull kelp is typically only found in more exposed areas, where *Macrocystis* abundance is low. Bull kelp also displays a temporal dynamic consistent with a ruderal species (e.g., rapid population in response to disturbance and light availability, eventual replacement by other species (Foreman 1977b)).

Figure 5. Photo by Terril Efird

Epiphytes: A wide variety of different epiphytic algae and invertebrates colonize *Nereocystis*; over 50 species of epiphytic algae have been documented on bull kelp blades and stipe, often showing distinct vertical distribution (Markham 1969). Common algal epiphytes include filamentous *Ulva/Enteromorpha* spp and *Antithamnion* spp, 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/recruitment with its host (Dickson and Waaland 1984; Dickson and Waaland 1985). Epiphyte cover on sporophytes increases over the summer through the fall/winter season, and can cause strong reduction in photosynthesis through direct shading of the blade. At high levels of epiphyte cover, this added weight may overcome the buoyancy of the pnuematocyst, and cause the entire alga to sink below the surface of the water, where light intensity is lower and blades are more likely to be in direct contact with grazers (CEQA 2001a). Epiphyte load leads to increased tattering of blades and may increase the likelihood of complete detachment during high wave force events 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 and Chess 1988). No estimates of either sporophyte mortality or reduction in photosynthesis/ 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 which affect other brown alga and can result in substantial loss of biomass through degradation and abscission of stipes and blades (CEQA 2001a).

Community ecology - role in coastal marine ecosystems

1. 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, for instance, modification of water flow and the delivery of larvae and other plankton, harboring prey and predators of other species in a community, trophic cascades (i.e. fueling grazer or detritus-based trophic pathways). Whereas such interactions have been the focus of numerous studies on *Macrocystis*, similar studies involving *Nereocystis* are few.

Macroalgae : As described in the previous section on biotic factors that limit the distribution and abundance of *Nereocystis*, the general conclusion is that *Nereocystis* is competitively inferior to many other algae (Foster and Schiel (1985) and others cited above). 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,

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though 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 above). 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 utilize bull kelp canopy and stipe 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 and Schultz 1973; Foster et al. 1979; Gotschall et al. 1984, 1986). The benthic invertebrate assemblage associated with *Nereocystis* is similar to that found associated with other annual kelp. Gotschall et al. (1984) documented lower invertebrate abundances around *Nereocystis* than *Macrocystis*, with the notable exception of red and purple urchins, which were more than twice as dense under *Nereocystis* beds. Also like giant kelp, the holdfast of bull kelp provides habitat for a large number and diversity of small invertebrates, including brittle stars, crabs, and small abalone (Andrews 1925), and may serve an important nursery function for juvenile invertebrates (sensu Beck et al. 2001); however, this has not been rigorously tested.
Calvert (2005) and Calvert et al. (in prep) conducted the only large-scale (1500m^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 for invertebrates distributed in either the surface or bottom portion of the water column. However, their sampling of invertebrates 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 west coast of North America, a great deal of research has been conducted on the relationships between macroalgae and fishes. However, much of this research has focused on interactions between fishes and the giant kelp, *Macrocystis spp.*, and far less attention has been given to the bull kelp, *Nereocystis.* Nonetheless, a few studies have described the relationship between fishes and bull kelp throughout its range. Like other taxa, the relationships between fishes and bull kelp can be divided into trophic and structural interactions and between the juvenile and adult stages of fishes.

The strongest relationships between macroalgae and fishes reflect the importance of habitat structure created by macroalgae for the juvenile stages of fishes. Though a number of studies have described the importance of algal structure as habitat for larval settlement and refuge from predators (see reviews by Carr and Syms (2006) and Steele and Anderson (2006)), almost all of this work has focused on the giant kelp, *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 were 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.* Four 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 and Richards 1987). Haldorson and Richards (1987) 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. Webster et al. (unpublished PISCO data, Carr per. comm.) surveyed fish assemblages associated with *Nereocystis* forests along the central coast of Oregon. Very high numbers of juvenile rockfish, including copper (and perhaps quillback, *Sebastes maliger*), and fewer juvenile black, *Sebastes melanops*, rockfish were observed both in the canopy and on the bottom at multiple forests. Similarly, Bodkin (1986) observed aggregations of juvenile rockfish (various species combined) at mid-depth and on the bottom of a *Nereocystis* forest in central California. In that study, use of the canopy habitat specifically is unknown because he did not sample that portion of the water column. Leaman (1980) mentioned that juvenile stripe surfperch, *Embiotoca lateralis*, were more abundant within the *Nereocystis* forest compared to habitat adjacent to the forest. 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 the kelp (e.g., (Carr 1989; Carr 1991; Carr 1994). To date, only two studies have conducted manipulations of *Nereocystis* with the possibility of assessing its effect on recruitment of juvenile fishes (Calvert 2005; Leaman 1980). While both studies identified effects on adult fishes, especially small cryptic species, neither detected strong effects on the density of young recruits as described by the observational studies mentioned above.

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, Southeast Alaska and Prince William Sound, AK, 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 compared fish assemblages between *Nereocystis* and *Macrocystis* forests (see below), but did not compare reefs with and without *Nereocystis*. Leaman (1980) compared reefs with and without *Nereocystis* and noted that three benthic (bottom-associated) species were particularly associated with the *Nereocystis* plants: the sculpin, *Synchirus gilli*, the snailfish, *Liparis spp.*, and the blenny, *Phytichthys chirus*. All three species are small (less than 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*, as it deposits its eggs directly on the pneumatocysts. Dean et al. (2000) compared fish assemblages among nearshore habitats, including a variety of algal habitat. They found distinct fish assemblages associated with habitats of different vegetation and exposure; the most abundant demersal fishes within eelgrass beds were juvenile Pacific cod, greenlings, and gunnels, whereas pricklebacks and sculpins dominated in *Agarum-Laminaria* point 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 appears to contribute to 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 neritic and demersal 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 demersal species but decreased the abundance and number of species 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 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 indicates that both demersal and neritic fish assemblages respond to the removal of a *Nereocystis* canopy and that differences in the response of the two assemblages to canopy removal depends on the location of canopy removal within a forest.

Calvert (2005) and Calvert et al. (in prep) 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 sub-canopy present and that the removal of the canopy decreased the local abundance of fishes. However, as Leaman (1980) found, this effect varied between the demersal and neritic fish assemblages. Upon manipulation of the kelp canopy, significantly greater abundance and biomass of benthic fishes occurred at sites with *Nereocystis* than sites without. In contrast, a direct negative effect of *Nereocystis* was observed for schooling fishes; six times more schooling fish (juvenile Pacific cod, *Gadus macrocephalus*, and walleye pollock, *Theragra chalcogramma*) were observed at sites without canopy kelp as compared to *Nereocystis* sites. They also noticed that 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 appears 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 demersal (i.e. bottom-associated) 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 (those that occur in the water column above the rocky reef) in *Macrocystis* than *Nereocystis* forests. Though 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, either by feeding on a) increased numbers of prey that graze directly on the *Nereocystis* plants (e.g., snails and amphipods), b) prey that feed on detritus produced by the canopy that detaches and falls to the floor of the forest, or c) species associated with the algae (e.g., juvenile rockfishes as described above). However, no studies examined this specifically in regard to the presence or abundance of *Nereocystis*.

2. 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 ecosystem via allochthonous export of biomass. *Nereocystis* production can be exported to other marine ecosystems (e.g., marine canyons, sandy beaches, rocky intertidal) 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 (Harrold et al. 1998; Kim 1992; Vetter 1995), and can influence community dynamics by changing the bacterial community (e.g., Tenore et al. (1984)) and providing refugia (e.g ., Norrko 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 habitat varies spatially, likely with local oceanographic features and with substrate characteristics (e.g., Orr et al. (2005)). Commensurate with *Nereocystis'* rapid growth, decomposition of lamina tissue is relatively rapid (Smith and Foreman 1984); however, the impact of *Nereocystis* in detrital pathways has not yet been studied quantitatively across ecosystems.

III. 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 specialty food product, and the dried parts are used for arts and crafts (Kalvass et al. 2004). Bull kelp is very similar to wakame (*Undaria pinnatifida*) used in traditional Asian cooking and may have potential as a culinary substitute (Malloch 2000). *Nereocystis* 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. 2004). *Nereocystis* is not used in the spawn on kelp industry because unlike *Macrocystis*, female herring will not deposit their eggs onto the fronds of bull kelp.

Figure 6.

In contrast to *Macrocystis*, for which harvesting involves removal of tissue from the upper four feet of canopy and leaves the rest of the plant essentially intact and capable of continued vegetative growth and reproduction, harvesting of bull kelp often involves the removal of the pneumatocyst and associated fronds (see Figure 6). By removing most of an individual plant's photosynthetic and meristematic tissue this method of collection eliminates the potential for further vegetative growth and eventually kills the plant by removing its source of buoyancy and causing the stipe to sink to the benthos (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 of the extent of bull kelp canopy cover in harvested beds. To avoid these outcomes it has been recommended that harvesting a) involve only the removal of distal portions of the fronds to allow for vegetative regrowth of adult plants, and b) be timed according to the reproductive schedules of the plants such that collection does not occur prior to 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 bull kelp.

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 one 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 were no harvesting occurred. While the results suggest that harvesting has no measurable effect on temporal patterns of plant density or mean plant biomass, the limited replication and short duration of the experiment (2-3 plots, 6 years total with 2 years of post-manipulation 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 bull kelp 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 post-harvest 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 as well as the number of reproductive propagules contributing to recruitment to the bed in subsequent years.

1. California

i. History of Harvest – California

Kelp has been harvested commercially off the California coast since the early 1900's. 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 lest 95% of the state's annual harvest. The company has been in operation since 1929 and by 2002 had acquired lease rights to 15 beds (~28 sq. mi.) 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 target 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 bull kelp 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 bull kelp 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 (CDFG 2001). Based on estimates of local *Nereocystis* abundance in this region, their harvest limit was set at 821 tons/year (CDFG 2001). Peak harvest by this firm was only 149 tons in 1999 and collection dropped substantially thereafter, with only 11 and 44 tons landed in 2000 and 2001, respectively (harvesting statistics are given in a table in (CEQA 2001a). This decline has been attributed to decreasing demand rather than reduced availability of the resource (Kalvass et al. 2004). As of 2002, only three of the state's 13 *Nereocystis*-dominated beds were open to harvest, and only one is currently leased to a commercial harvesting operation (bed 312, to Abalone International).

ii. Historical and Current Stock Assessment - California

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) in 1912. Historical records of bull kelp abundance are limited because subsequent surveys did not differentiate between *Macrocystis* and *Nereocystis*. Additionally, 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 bull kelp 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. 2004). While the 1912 and 1989 surveys estimated ~6.5 sq. mi. of bull kelp canopy north of Point Montara, the 1999 survey indicated a decline of ~42% decline in kelp coverage in the area between Point Montara (San Mateo County) and Shelter Cove (Humboldt County) (CDFG 2001). This apparent decline, which runs counter to observations of extensive beds in this region in late 1999, may be attributable in part to a) the timing of the 1999 survey, which occurred after a major storm, b) improved interpretation methods for aerial photos, and/or c) natural fluctuations

in kelp bed coverage and density (Kalvass et al. 2004). On a more local level, the Crescent City harvesting operation conducted a 1996 survey of bull kelp abundance in bed 312 as part of their harvesting least agreement with CDFG. They estimated 5,475 tons of *Nereocystis* in the 205 acres of bed 312 between Point St. George and Whaler Island.

No recent bull kelp surveys have been conducted in central California. Results of the 1912 survey suggest that 32% of the 17.55 sq. mi. kelp canopy in this region was associated with *Nereocystis* (Kalvass et al. 2004). In central California, bull kelp seems to be outcompeted by *Macrocystis* and is generally restricted to area a) on the outer fringes of giant kelp beds, b) within the surge zone, or c) from which giant kelp has temporarily been removed by disturbance associated with winter storms or strong waves. Evidence of the temporally dynamic nature of bull kelp abundance comes from Diablo cove, where density levels declined from 200 tons/acre in 1975 to 4.8 tons/acre in 1982 (Kalvass et al. 2004).

iii. Management and Recent Harvest - California

California's kelp bed management, a responsibility of CDFG, has focused mostly on giant kelp. Collection of kelp for commercial purposes requires a 1-year, $100 license, and harvesters are required to keep collection records (see below). Kelp beds may be leased from the State Land Commission for up to 20 years with a deposit of no less that $40 per square mile. Leased areas may not exceed 25 sq miles or 50% of the total kelp resource, whichever is greater (Mackey 2006). There is a royalty for edible seaweeds of $24/wet ton 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 collection targets *Nereocystis* for human consumption, the harvest limit is 2 tons per 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 surface water (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. 2004; Mackey 2006). Although these harvest summary data have been collected on a regular basis 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 one year if it is determined that the bed is being damaged by collection, the information necessary for detect detrimental impacts of harvest on kelp resources is largely unavailable (Kalvass et al. 2004). Given these management resources the CDFG commission took formal precautionary steps to protect kelp beds in northern California (esp. bull kelp) in 1996:
- Extended the kelp bed numbering system initiated in 1915 for beds in southern and central California by adding a 300-series designation for kelp beds north of San Francisco

(Kalvass et al. 2004; Little 2002). These beds are composed primarily of bull kelp. Prior to this action, because of the lack of formal CDFG recognition, any northern bed could have been harvested for commercial purposes.

- Closed beds 303-307 to future commercial harvest
- Limited the remaining beds in the 300 series to a max harvest of 15% of the biomass as determined by a DFT-approved annual survey conducted by the lessee.

In 2001 the commission added further restrictions (Kalvass et al. 2004):

- Closed beds 301, 302, 310, and 311. Harvesting of bull kelp is restricted north of Point Arguello by California code of regulations: title 14, section 165(c)(4) (MBNMS 2003)
- Restricted the harvest from April 1 through July 31 within the Monterey Bay National Marine Sanctuary
- Required harvesters 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)
- Created commission 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 5 active commercial permits in California for *Macrocystis* harvest and none for commercial harvest of bull kelp (Mackey 2006). A 3-year 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).

2. Oregon

i. History of Harvest – Oregon

The only recent documented commercial harvest of *Nereocystis* in Oregon occurred from 1988 through 1992, when a company collected ~70 tons of tissue from kelp beds associated with Orford Reef in southern Oregon (Kalvass et al. 2004; Mackey 2006). A 5-year 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.

ii. Historical and Current Stock Assessment - Oregon

We were unable to find any information on the past or present abundance of bull kelp off the Oregon coast.

iii. Management and Recent Harvest - Oregon

The DSL has jurisdiction over submerged subtidal lands (any land "lying below the line or 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). Up to 40 miles of submerged land may be leased to a single individual for a period of no more than 50 years with no stated restrictions of the amount of kelp that may be harvested during the lease

period. Persons collecting less than 2,000 pounds of kelp per year 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, field work, 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 is a single active lease for kelp harvest in the intertidal zone of southern Oregon by James Jungwirth. This permit is set to expire in mid 2006 and associated harvest should not involve *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).

3. Washington

i. History of Harvest – Washington

We were unable to locate any evidence of attempts to commercially harvest bull kelp in Washington State.

ii. Historical and Current Stock Assessment - Washington

Members of the Nearshore Habitat Program of the Washington Department of Natural Resources (WDNR) 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 Washington's outer coast from Port Townsend to the Columbia river (~360 km of total shoreline) (Berry et al. 2001). Data are collected according to the following protocol. First, color-infrared photographs of the survey areas, taken at 1":2500' scale, are collected from a fixed wing aircraft using a 70 mm camera (see Figure 7). The annual inventory is completed in late summer in order 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, surface winds less than 10 knots, sea/swell less than 5 feet, sun angle greater than 30 degrees from vertical, cloud and fog-free skies.
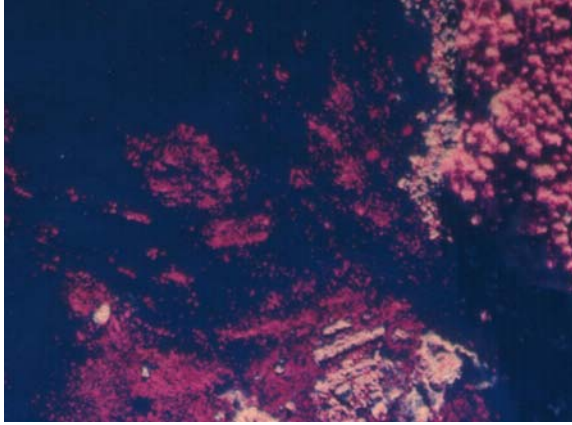
Figure 7. A sample of color-infrared imagery collected as part of the surveys. Floating kelp canopies appear as red areas on the dark water surface. Photo interpretation is used to classify red floating kelp as canopy area. Bed area is delineated by grouping classified kelp canopies with a distance threshold of 25 m. *Courtesy of Helen D. Berry, Nearshore Habitat Program, Washington State Department of Natural Resources*

Next, photos are projected onto 1:12,000 topographic maps using a slide projector and the outline of kelp beds transfer by hand (see Figure 8). Maps are scanned and digitized, and two parameters are estimated: **Canopy Area** is the area at the water surface covered by *M. integrifolia* and *N. luetkeana* plants (stipes, bulbs and blades). **Bed Area** is the area covered by the entire bed (including both plant fronds and gaps between plants). A distance threshold of 25 m was used to determine whether plants were grouped into a bed. The bed area parameter is sometimes called 'planimeter area' because it is similar to the historical kelp mapping methods that encircle an entire bed, including plants and gaps. The method does not produce rectified imagery with high positional accuracy. One strength of this method is that it is relatively rapid and relatively inexpensive when compared to methods using conventional 9 inch x 9 inch photography and rectified imagery. Another strength is consistency in methods. The same methods have been employed since 1989, and the same person has collected and analyzed the data since 1989 (WDNR 1999).

Figure 8. Study area for long term monitoring of canopy-forming kelp in Washington State conducted by the Department of Natural Resources.

Analyses of data collected between 1989 and 2000 reveal 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. Bull kelp also may be more sensitive to climate anomalies: during the 1997 El Niño event, *Nereocystis* populations along the outer coast experienced a 75% reduction in size as compared to 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.

iii. Management and Recent Harvest - Washington

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" and in light of its biological importance and economic value, urged the implementation of stricter harvesting regulations (Mackey 2006). At the present time 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 bull kelp, fronds are to be cut no closer than 24 inches above the pneumatocyst using a knife or similar instrument (Hillmann 2005). There are 3 types of non-scientific collection permits in Washington: *annual combination permits* allow for harvest of seaweed, shellfish, and both fresh and saltwater fish, *annual shellfish and seaweed permits* allow for harvest of seaweed and shellfish, and *1-5 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 number of active permits of these types was 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 for "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/agencies, further protecting coastal environments from commercial harvesting (Mackey 2006).

4. British Columbia

i. History of Harvest – British Columbia

The first attempt at commercial harvesting of marine plants in British Columbia was undertaken by Canada Kelp Co., Ltd. in 1949. Financial complications led to the failure of this endeavor 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-year 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 tons per year (from Malloch (2000) and Wheeler (1990)).

ii. Historical and Current Stock Assessment - British Columbia

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 that uses aerial photography to estimate the

area, density, and species composition of kelp beds (Foreman 1975). 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, 12 surveys covering the majority of kelp beds that could support large-scale harvesting had been completed. Approximately 94% of the standing stock in these beds consisted of *Nereocystis*. As part of a study at Malcom Island, Foremen (1984) concluded that KIM-1 estimates were generally proportional to standing crop values but tended to overestimate these values by ~30%. More detailed descriptions of the survey methodology can be found in (Foreman 1975; Wheeler 1990).

List of kelp bed surveys (mixed beds) in British Columbia using the KIM-1 method

Inventory Area	Year	Length of Inventoried coastline (km)	Bed area (ha)	Total Standing Crop (wet tones)
Procher, Goschen, and Banks Islands and Estevan Group[1]	1996	70	1,090	59,652
Hakai Passage to Bardswell Group[2]	1993	106	1,550	55,224
Vancouver Island and Malcolm Island Shores of Queen Charlotte Strait[3]	1989	40	761	37,934
Juan de Fuca Strait[4]	1988	118	511	50,148
Northwest Vancouver Island[5]	1978	72	840	48,615
Estevan Group[6]	1976	82	1,470	77,620
Dundas Group[7]	1976	61	1,527	74,350
North Graham Island (QCI)[8]	1976	162	2,375	77,410
Goschen Island to Tree Nob Group[9]	1976	122	1,741	113,575
North Vancouver Island[10]	1976	68	885	38,020
Nootka Sound[11]	1995	57	850	73,836
Nootka Sound[12]	1975			
1. (Sutherland 1998) 2. (Field 1996) 3. (Sutherland 1990) 4. (Sutherland 1989) 5. (Coon et al. 1982) 6. (Field et al. 1977) 8. (Coon et al. 1979) 9. (Coon et al. 1980) 10. (Coon et al. 1981) 11. (Sutherland 1999) 12. (Coon and Field 1976)				

iii. Management and Recent Harvest - British Columbia

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 transfers 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 1) the overall operation is economically feasible, and 2) the raw material requirement is low either in absolute terms or compared to 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 20cm 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 spawn on kelp (SOK) industry). Non-commercial harvesting is unregulated, and this poses a problem for enforcement of management regulations since the intended use of harvested materials is not always clear. More recently 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).

5. Alaska

i. History of Harvest – Alaska

We were unable to locate any information on historical harvesting of bull kelp in Alaska.

ii. Historical and Current Stock Assessment - Alaska

The only comprehensive assessment of canopy forming kelp in Alaska was the "potash from kelp" survey carried out by the USDA in 1913. In southeast Alaska 1133 beds, with an estimated area of 18,300 hectares and biomass of 7.15×10^6 metric tons, were counted. Of these beds, 87% were comprised principally of *Nereocystis*, 6% of *Macrocystis*, and 7% of *Alaria fistulosa*. In the northern Gulf of Alaska, 358 beds, representing an estimated 4,610 hectares and 3.26×10^6 metric tons, were recorded. Here, *Nereocystis* made up approximately 55% of the beds, with the remaining 45% being *A. 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 spawn on kelp industry, but these rarely involve *Nereocystis* since herring will not spawn on bull kelp (Dr. Michael Stekoll, pers com 2006).

iii. Management and Recent Harvest – Alaska

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 (Dr. Michael Stekoll, pers com 2006). 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-spawn-on-kelp is subject to different regulations ((Hansen and 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 and 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 and 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 ton per year (Brian Pierce, pers com 2006). Another company, the Alaska Kelp Company out of Point Baker, Alaska was issued a *Nereocystis* harvest permit from the Petersburg ADFG office for 200,000 pounds per year. 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* sold under the names "Opticrop", "Garden Grog" and "Alaska Kelp". One year they sold about 10,000 tons 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 (Dr. Michael Stekoll, pers com 2006).

Pollution

1. 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 conducted temperature sensitivity experiments using bull kelp in 1982. Under laboratory conditions, juvenile sporophytes were exposed to water temperatures ranging from 10°C to 20°C for 44 days. Results indicated that prolonged exposure to water temperatures above 18°C is lethal. Further, 25% of the plants held at 15.9°C died after 36 days. A primary cause of mortality appears 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 power plant's thermal discharge plume experienced premature blade loss, and *Macrocystis*, a more heat-tolerant species, eventually colonized those sites. Bull kelp 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 (CEQA 2001a). These observations were supported by a comparative study performed by Shiel and colleagues in this system. Using an 18-year intertidal and subtidal monitoring program and before-after control-impact (BACI) analyses, Shiel et al. (2004) demonstrated quantitatively that bull kelp density and abundance were significantly reduced by a 3.5°C rise in water temperature associated with thermal discharge from the Diablo Canyon plant.

2. Sediment/nutrient runoff: (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, above, and discussion in (CEQA 2001a). Reductions in light penetration could result from a number of processes that increase water turbidity. Sewage discharge and nutrient runoff associated with agriculture could trigger phytoplankton blooms that significantly reduce water clarity. Particulate runoff 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 substrate 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 bull kelp density in areas associated with landslides (Konar and Roberts 1996; Shaffer and Parks 1994). Burge and Schultz (1973) observed an increase in water turbidity in Diablo Cove, CA following exceptionally heavy rains and associated runoff during the winter of 1968-69. *Nereocystis* sporophytes were not seen in the area again until mid July of 1969, and the reemerging bed was reported to be one-quarter the size of the bed in 1968. This reduction in bull kelp abundance was attributed to changes in nearshore light levels (discussed in (CEQA 2001a). The large pulse of freshwater runoff 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 bull kelp sporophytes develop blisters and wilt when subjected to rapid reductions in environmental salinity.

3. Toxic chemicals

Very little is known about the effects of toxic chemicals on bull kelp. 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 (CEQA 2001a). Antrim et al. (1995), in tests of the effects of diesel fuel, intermediate diesel fuel (IFO) and crude oil on *Nereocystis* plants, verified that exposure to petroleum products have a negative effect on bull kelp. Severe tissue necrosis occurred at meristematic tissue between the stipe and bulb. In contrast to these results, comparisons of bull kelp biomass and percent cover between oiled and control sites in Prince William Sound, AK,

following the Exxon Valdez oil spill, did not indicate any effects of petroleum exposure. Bull kelp individuals at oiled sites tended to be smaller, but it was not clear whether this was due to chemical toxicity or natural factors such as recent recruitment or slow growth (discussed in (CEQA 2001a).

Human modification of species interactions

Human introduction of non-native species into kelp forest ecosystems have the potential to modify species interactions in ways that affect the distribution and abundance of bull kelp. The invasive macroalga *Sargassum muticum* is a potential example of this. 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 bull kelp from these locations under some circumstances (Thom and Hallum 1990). *S. 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 and Lindstron 2000).

More important to bull kelp 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*) and red abalone (*Haliotis rufescens*; see Population Ecology Section above), all species that are currently harvested, and also fluctuate in density in response to sea otter population dynamics (Vanblaricom and Estes 1988). Native or naturalized epiphytes growing on bull kelp can negatively impact kelp growth and survival (see Population Ecology section and references therein); such epiphyte effects could be particularly pronounced in areas where elevated nutrient concentrations that promote growth of epiphytic algae.

Climate change

1. Episodic El Niño events: temperature changes and storms

The reduction in upwelling and increased frequency of severe storms and strong wave action associated with El Niño events could all have negative impacts on the distribution and abundance of bull kelp. Suppression of upwelling reduces the amount of cold, nutrient water brought into shallow subtidal areas from depth (CEQA 2001a) and can lead to warming of surface waters by up to 4°C for extended periods (McPhaden 1999). As mentioned previously, *Nereocystis* is sensitive to increases in water temperature, and the availability of nutrients, particularly nitrogen in the form of nitrate, is perhaps second in important only to light availability as a necessary condition for the growth and reproductive maturation of bull kelp. Perturbations in the physical environment associated with El Niño events thus have the potential to drive reductions in bull kelp abundance and recruitment on interannual timescales. Delayed recruitment and reduced growth of bull kelp in the beds near Fort Bragg, CA in 1992 may have been associated with the El Niño event of that year (Kalvass et al. 2004). During the 1997 El Niño event, total kelp canopy in Washington decreased by 32%. Bull kelp populations along the outer coast were reduced by 75% (compared to only 8% reductions for *Macrocystis*).

While mortality associated with strong storm events and wave action also have the potential to reduce the size of *Nereocystis* beds, the weedy nature of bull kelp might allow the species to rapidly recolonize impacted areas following the removal of more competitively dominant species of algae such as *Macrocystis*. In 1998, following the reductions in bull kelp abundance in Washington described above, *Nereocystis* populations rebounded dramatically, increasing by 423% (Berry et al. 2001). This may be evidence a positive effect of storms on bull kelp 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 strong storm and wave disturbance on bull kelp.

2. Long term global warming impacts

Because of its sensitivity to water temperature and preference for cold conditions, *Nereocystis* would likely by adversely affected by increases in sea surface temperature associated with global warming. No data to quantitatively substantiate this speculation are available. Changes in the CO_2 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 CO_2 in nearshore marine environments could influence growth rates of photosynthetic organisms. One short terms study showed that doubling ambient CO_2 concentrations for 2 hours increased the net apparent photosynthetic rate of *Nereocystis* by a factor of between 2.2 and 2.8 (Thom 1996). Temperature-related increases in bull kelp mortality could thus be offset to some extent by enhanced growth under conditions of greater CO_2 availability.

Incidental damage

Commercial fishing activities can cause directly 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 (CEQA 2001b). Additionally, 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 substrate. 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 and/or chronic, the extent of kelp damage due to boats and fishing gear is thought to be minimal (CEQA 2001b).

IV. RECOMMENDATIONS FOR MANAGEMENT AND RESEARCH TO INFORM MANAGEMENT DECISIONS

Overview and challenges for managing the harvest of *Nereocystis*

In contrast to *Macrocystis*, the 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 bull kelp. To some extent this is understandable since harvest pressure on bull kelp 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 bull kelp across the entire extent of the species' range. We were unable to find any quantitative records of personal (non-commercial) take, 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 a) natural fluctuations in the abundance of bull kelp, or b) effects of harvesting on the demography of *Nereocystis* populations. Aside from recently but spatiotemporally 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, we found only three studies that directly examined the effects of harvesting on *Nereocystis* growth, reproduction, or population dynamics. Two of these involved such limited replication that the results cannot reasonably be used to inform sound management policies. Additionally, because of the fundamental life history differences between giant and bull kelp we would expect the demographic impacts of harvesting on these two species to be fundamentally different and question the extent to which our understanding of *Macrocystis* can be used to create sound policies for the harvest of *Nereocystis*.

The exceedingly superficial understanding of *Nereocystis* demography and the effects of harvest may be a principle cause of the dramatic variation in bull kelp management regulations in the different political provinces where the species is found. In northern California, commercial harvesting in the 300-series beds that are comprised mostly of *Nereocystis* is forbidden or severely restricted. North of the border in Oregon, leases of subtidal lands, which can last for up to 50 years, are not accompanied by any restrictions on the amount of kelp that can be commercially taken. Personal collection of up to 2000 pounds of tissue does not require a permit. Further north, Washington State has arguably the most conservative and scientifically sound management policies (Berry et al. 2005; Berry et al. 2001). 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 bull kelp. In spite of these relatively detailed stock assessments, the state of Washington prohibits the commercial harvest of bull kelp and limits personal take to 10 pounds per permit per day. 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 1970's, but most of these are limited in their geographic breadth and do 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 re-approved 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 next to impossible 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 in order for scientifically sound management policies to be enacted. First, more basic research needs to be done to characterize natural demographic dynamics of bull kelp beds and quantify the effects of harvesting on these dynamics. Data generated by more regular and comprehensive stock assessment surveys can be used by the government 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 location(s) and capacity requirement of their facilities. Studies of the impacts of harvesting on bull kelp physiology, growth, and demography are critical for the development of management policies that will sustain both the profitability of commercial harvesting operations as well as the fundamental ecological patterns and process associated with bull kelp beds. Second, greater methodological and legislative consistency among management entities in 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 makes 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 regulating and monitor the impacts of harvesting will facilitate a) comparison of data from different geographic regions since information is collected using the same methods, b) maintenance of more comprehensive and intelligible databases on stock assessments and harvest levels, and c) enforcement of harvest regulations since broadly adopted policies reduce uncertainty about local regulations for both collectors and enforcement agents.

Research recommendations

Using our synthesis of the literature presented above, we have 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 a) the status, dynamics and use of *Nereocystis* populations, b) impacts of harvest on the sustainability (resilience and replenishment) of *Nereocystis* populations, c) impacts of harvest of *Nereocystis* on shallow reef ecosystems, and d) impacts of harvest on other coastal marine ecosystems. We introduce these recommendations in the order that we believe they should be prioritized.

A. Stock/resource assessment methodologies:

Central to any resource management program 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. However, the accuracy and precision of these estimates has not been assessed, nor has variation in factors (e.g., sea conditions, atmospheric conditions, timing) that influence these estimates been examined. Surveys to test the functional relationship between diver-based estimates of plant density and biomass with estimates of abundance from aerial surveys would provide ground-truthing of the aerial-based estimates and perhaps allow translation of canopy cover to biomass estimates. Thus, we recommend a well-designed study of the use of aerial digital imagery as a foundation for a more comprehensive stock assessment. Like other recommendations below, 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.

B. Potential impacts of harvest on the resource:

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 vs. mechanical harvest; whole plant vs. partial blade; the relative extent (% 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 reestablishment of a forest? Can the impact of harvest on growth and reproduction of *Nereocystis* be minimized by timing harvest according to forest phenology? Does forest phenology vary geographically, and how? Because some literature hints at the possibility of spores over-wintering (a biennial, rather than annual reproductive cycle), further exploration of this should be conducted to determine if generations can overlap. Equally important will be the identification of one of 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 a) directly linked to demographic patterns/rates associated with the bull kelp population(s) being harvested, and b) easy to measure. Finally, indirect effects of harvesting on the distribution and/or abundance adults, manifest via impact(s) 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 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).

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 neighboring 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 on their size and isolation. There is evidence that *Macrocystis* spores must settle at a threshold density to ensure successful fertilization between the male and female gametophytes. At lower densities gametophytes are separated from one another too far for sufficient encounter of eggs and sperm. Whether this

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"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 also would be useful in identifying regions with unique genetic composition, with an eye toward preserving the genetic diversity of the species.

C. Potential impacts of harvest on kelp forest ecosystems

Our 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, little rigorous assessments of the presence or density of *Nereocystis* on the structure and functions of the algal, invertebrate or fish assemblages have been conducted. Because of the ephemeral occurrence and lack of structural complexity, *Nereocystis* may not be nearly as influential as *Macrocystis* has been shown to be on kelp forest communities. However, because it can be the only source of habitat that extends to the water surface and juvenile fish have been observed strongly associated with the 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 primary production and detritus for key species in shallow reef ecosystems (e.g., sea urchins, abalone). Some key questions that remain unanswered are: 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 (this 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., 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.

D. Potential impacts of harvest on other coastal marine ecosystems:

Like *Macrocystis*, the great amount of biomass produced and lost from forests each year can be transported to adjacent ecosystems onshore (e.g., sandy beaches, rocky intertidal) and offshore (e.g., deep rocky reefs, submarine canyons) where it fuels a detritus-based trophic pathway and creates temporary habitat structure. The magnitude and consequence of this connectivity among ecosystems is poorly understood. What is the role of *Nereocystis* in ecosystem connectivity between the 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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