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Chapter 8

Diversity and Dynamics of Californian Subtidal Kelp Forests

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Introduction to the environment

Californian kelp-forest ecosystems are highly diverse and productive and are one of the most distinctive features of the Californian coastline. They have also served as the focus of innumerable experimental and observational studies by ecologists interested in processes structuring nearshore marine systems. Despite over 50 years of intensive field and laboratory research, however, much remains to be understood about the processes that determine their diversity and dynamics. In particular, food web structure of communities associated with the giant kelp (*Macrocystis pyrifera*) has received little attention (Rosenthal et al. 1974, Pearse and Hines 1976, Foster and Schiel 1985, Schiel and Foster 1986, Graham 2004), due in no small part to the apparently complex nature of these systems. Since Darwin (1839), it has been generally perceived that much of the structure and diversity of these systems is due to the presence of giant kelp itself (reviewed in Graham 2004). Yet, it is still unclear whether this role of giant kelp is due to its high levels of energy production, its provision of complex habitat, or simply a by-product of the inherently diverse and productive coastal environments in which giant kelp is found. This chapter introduces the reader to the diversity and dynamics of Californian kelp forest food webs and explores the methodological and theoretical challenges of studying the processes structuring kelp forest communities.

Geological History

A diverse array of geological processes has shaped the Californian coastline (reviewed in Legg 1991), establishing the regional physiography and geologic substrate composition. To begin with, the narrow continental shelf, deep ocean trenches, and steep mountain ranges that define much of California's coastal geomorphology are consequences of the subduction of various oceanic plates beneath the North American continental plate. Unlike most other regions of the world, however, this region was subsequently transformed into a strike-slip fault system, caused by the collision of an eastward migrating mid-ocean spreading center with the subduction zone, beginning ~40 million years BP. The transformation was most dramatic south of Point Conception (Fig. 1), where uplift, subsidence, rotation, compression and extension due to faulting and tectonics resulted in a mosaic of basins, islands and offshore banks embedded within a widened region of the continental shelf. Subduction ceases north of Point Conception, although the coastline there remains relatively linear and the continental shelf relatively narrow. Substrate composition can vary over short spatial scales (kms) in California, from basaltic, granitic or sedimentary rocks to gravel and sandy beaches (Greene and Kennedy 1986, 1987, 1989). Extensive rocky platforms are more common north of Point Conception, whereas large sandy beaches are predominant to the south (Graham et al. 2003). Consequently, kelp forests north and south of Point Conception inhabit regions of fundamentally different geomorphology.

Northeast Pacific Oceanography

In California, coastal oceanographic parameters important to the establishment of kelp forests (e.g. temperature, nutrients, wave action) are controlled primarily by variability in a cool southward-flowing eastern boundary current, the California Current, partially linked to swings in the Pacific Decadal Oscillation (for example Chelton and Davis 1982, Lynn and Simpson 1987, Lluch-Cota et al. 2001, Batchelder and Powell 2002, see also contributions to Vol. 50 of Deep Sea Research II, 2003). During periods when the Aleutian low-pressure system is weak, spring equatorward winds and the flow of the California Current are strong, and oceanographic productivity is fuelled by longshore transport of nutrients from upwelling regions at coastal promontories. As the Aleutian low strengthens or winds weaken during the fall, a poleward-flowing counter-current (the Davidson Current) often develops, bathing the coast in warmer, more nutrient-depleted waters. Consequently, seasonal fluctuations in sea-surface temperature, nutrients, and productivity are ubiquitous features of the Californian coast (Hickey 1998; Fig. 2).

As with coastal geomorphology, however, differences in coastal oceanographic conditions can be striking north and south of Point Conception (Hickey 1998, contributions in Vol. 50, Deep Sea Research II, 2003). In southern California, a semi-permanent cyclonic gyre exists that incorporates California Current water with warmer waters intruding from the southeast (Hickey 1993). As such, seasonal fluctuations in oceanographic conditions are generally much greater south of Point Conception (Fig. 2); e.g. summer-fall sea-surface temperatures average >18˚C in southern California but <15ºC in central California. Greater distance from the Aleutian low, and increased protection by Point Conception and offshore islands, also result in a more benign wave environment in southern California (Fig. 2). Finally, episodic ENSO events (~4-7 year periodicity) substantially alter oceanographic conditions in California by enhancing the poleward flow of warm waters, shutting down upwelling, raising nearshore sea levels, and increasing wave intensity (Ware and Thompson 2000). For kelp systems, each of these ENSO effects increases in severity from north to south (Edwards 2004), except wave intensity, which exhibits the opposite trend. These marked differences in the oceanographic conditions experienced by shallow coastal reefs north and south of Point Conception contribute to marked differences in the productivity and seasonal and interannual variability in kelp forest size and distribution (Edwards 2004).

Patterns of Biogeography and Biodiversity

The flora and fauna of Californian coastal waters are inherently rich, with current taxonomic resources describing approximately 650 macroalgal, 500 fish, 90 bird, 28 marine mammal, and 1000s of invertebrate species (Miller and Lea 1972, Smith and Carlton 1975, Abbott and Hollenberg 1976, Austin 1985, Ricketts et al. 1985, Briggs et al. 1987, Orr and Helm 1989). Overall species composition and diversity of these taxonomic groups differ greatly between the coastal waters of central/northern and southern California. In general, the warmer Californian biogeographic province to the south of Point Conception is enriched in fish, invertebrate, and macroalgal taxa of sub-tropical origin, and has a higher rate of endemism, relative to the cooler Oregonian province north of Point Conception. The region around Point Conception is a transition zone between the two provinces and some taxonomic groups increase in diversity there due to provincial overlap and inclusion of "transition zone" taxa (Newman 1979); numerous other biogeographic boundaries have been proposed along the Californian coast (reviewed in Dawson 2001). Many of these patterns in biodiversity and biogeography likely reflect historic and present patterns of geographic variability in geomorphology and oceanography, and it is within this physical gradient that Californian kelp forest communities have assembled and evolved.

The Food Web

Our objectives in constructing a general Californian kelp forest food web are three-fold. First, the food web presents an updated perspective on the general structure of trophic interactions within Californian kelp forests based on studies conducted since the last food web was constructed over 20 years ago (Foster and Schiel 1985). Second, in combination with a discussion of regional variation in common kelp forest taxa, the food web illustrates key similarities and differences in kelp forest associations between southern and central California. Finally, the patterns revealed from the food web can generate hypothesized roles of trophic interactions and habitat associations in structuring Californian kelp forest communities, and help guide process-oriented studies designed to test those hypotheses. In the first section (*Trophic guilds*), we (1) describe the members of each trophic level that create the food web and (2) introduce major differences in kelp forest species composition north and south of Point Conception. In the subsequent section (*Food web structure*) we evaluate key trophic and habitat associations and use the differences in such associations between southern and central kelp forests to suggest whether energy or habitat provision is structuring kelp forest systems, and to demonstrate possible experimental approaches that could be used to test these ideas.

Trophic Guilds

Producers

The energy base of Californian kelp forests is founded primarily upon subtidal kelps (Order Laminariales) of variable productivity potential and habitat architecture (Fig. 3). Of the six common subtidal kelp taxa in California, two species, *Macrocystis pyrifera* and *Nereocystis luetkeana,* are dominant in terms of their contribution to the formation of surface canopies, productivity and habitat structure. A third species, *Pelagophycus porra,* is less common, typically forms a canopy below the surface, and is found only in southern Californian (Druehl 1970, Abbott and Hollenberg 1976). The giant kelp *M. pyrifera* dominates shallow nearshore rocky platforms (< 25-30 m depth) in southern California and most regions of central California that range from moderately exposed to protected. The bull kelp *N. luetkeana* has a southern range limit to the north of Point Conception and is the primary canopy former in areas of high wave exposure (Foster and Schiel 1985). Of the three other prominent subtidal kelps, *Pterygophora californica* and *Eisenia arborea* form dense canopies 1-2 m above the reef surface, whereas blades of the more prostrate *Laminaria farlowii* lie across the surface of the reef; all three can be found both north and south of Point Conception. Together, these canopy, sub-canopy and prostrate taxa form successive layers in Californian subtidal kelp forests, with some taxa found only in particular regions, habitats, or depth ranges (for example deep-water kelps; Spalding et al. 2003). Beneath these various kelp layers is an exceedingly diverse group of red, green, and brown foliose, turfing, and encrusting algae (for example Breda and Foster 1985, Harrold et al. 1988, Graham 2004). In addition to high coverage of benthic substrate, the foliose and turfing algae provide key habitat and energy resources to diverse epifaunal assemblages that can be important food sources for higher trophic levels, including fishes (Limbaugh 1955, Quast 1968a, Bray and Ebeling 1975, Coyer 1985, Hallacher and Roberts 1985, Ebeling and Laur 1986, Hobson and Chess 1986, Coyer 1987, Holbrook et. al. 1997).

No studies have directly compared non-kelp macroalgal assemblages between central and southern California, but regional studies have identified 43 species common to kelp forests in southern California (Graham 2004) and >50 species common to kelp forests along the Monterey Peninsula in central California (Harrold et al. 1988); only 25 species of macroalgae were shared between these two Californian studies. The primary difference in non-kelp macroalgal diversity between these regions appears to be due to a decrease in species richness of red algae, and an increase in brown algae (primarily of the orders Dictyotales and Fucales), from north to south (for example contrast Foster and Schiel 1992 and Graham 2004 with Breda and Foster 1985 and Harrold et al. 1988). Each of these algal groups also contribute to an algal detrital pool (Fig. 3) that can be the primary conduit of fixed carbon into kelp systems (for example Gerard 1976, Pearse and Hines 1976, Harrold and Reed 1985, Duggins 1988, Duggins et al. 1989). Whether through attached or detrital pathways, it is generally accepted that, when present, *M. pyrifera* represents the single greatest source of fixed carbon to Californian kelp forests (reviewed in Graham 2004); it is also the primary structural component of the ecosystem.

Consumers

The prominent consumers in Californian kelp forests constitute five trophic categories: grazers, detritivores, planktivores, and lower- and higher-level carnivores (Fig. 3). The feeding habits of many consumer species defy strict categorization within a single feeding-category (Foster and Schiel 1985), as they acquire energy from a variety of trophic groups. For example, the highly abundant sea star *Asterina miniata* grazes the surface of rocky reefs and adjacent sand substrata, non-selectively foraging on benthic diatoms, macroalgal microscopic stages, algal and animal detritus, and sessile planktivores (for example barnacles, bryozoans; Pearse and Hines 1976, Leonard 1994). For most species, however, a review of the published literature identified clear primary trophic levels for consumers (Graham 2004), and assignment of species to these primary feeding-categories, as we do in the following sections, helps to identify key differences in trophic interactions within and between southern and central Californian kelp forests.

As with producers, there are conspicuous differences in the species composition of kelp forest consumers between central and southern California, mostly due to biogeographic differences in the major taxa. For example, reef fishes of tropically-derived families (such as wrasses, sea basses, damselfishes, and gobies) are all more abundant and diverse south of Point Conception, whereas fishes of temperate-derived families (including rockfishes, sculpins, greenlings, surfperches) are more abundant and diverse to the north (Miller and Lea 1972, Horn and Allen 1978, Stephens et al. 2005). In fact, the composition of consumer species can often differ greatly within regions in California, especially between the Californian mainland and Channel Islands, and among the Channel Islands (Ebeling et. al. 1980 and Patton et al. 1985 for fishes).

Planktivores and detritivores

In both southern and central Californian kelp forests, the combined contributions of the detrital organics produced by *Macrocystis pyrifera* (dissolved and particulate), and the constant influx of phyto- and zooplankton (for example mysids; Clarke 1971, Hobson and Chess 1976, Coyer 1985), support a striking abundance and diversity of filter and suspension feeding detritivores and planktivores (Harrold et al. 1988, Graham 2004). Particularly impressive among the detritivores and planktivores is the diversity of phyla, each of which in turn is represented by both high taxonomic diversity and abundance (e.g., tunicates, sponges and anemones, bryozoans, gastropod and bivalve molluscs, annelids, echinoderms, crustaceans, fishes). Some taxa are largely detritivorous, like the conspicuous and habitat-forming mounds of the colonial annelid *Diopatra ornata*, and some commercially sought sea cucumbers. Primarily planktivorous species are distributed throughout the water column, from the reef base to ocean surface. Those that position themselves well above the reef surface include a variety of fish species suspended in the water column (Hobson and Chess 1976) or sessile invertebrates attached to or closely associated with the surface of kelps and rocky promontories (for example mysids, caprellid amphipods, barnacles, and bryozoans; Wing and Clendenning 1971, Woolacott and North 1971, Bernstein and Jung 1979). The most conspicuous differences among the planktivores in southern and central Californian kelp forests are among the fishes. Notably abundant in southern California are gobies, halfmoon, blacksmith, senorita and several transient planktivorous species (for example *Salema*), all of which are members of tropically-derived families (Gobiidae, Kyphosidae, Pomacentridae, Labridae; Quast 1968a,b,c, Hobson and Chess 1976, Holbrook et al. 1990). In contrast, juveniles and adults of the temperate-derived rockfishes (genus *Sebastes*) are prevalent in central California (for example Miller and Geibel 1973, Hallacher and Roberts 1985, Singer 1985, Gaines and Roughgarden 1987, Carr 1991). One notable difference in benthic planktivores between southern and central Californian rocky reefs is the prevalence of gorgonians in southern California (e.g., *Lophogorgia chilensis*, *Muricea californica* and *Eugorgia rubens*; Gotshall 1994), again reflecting the influence of tropical taxa in this region. However, most species employ their suspension and filter-feeding mechanisms to consume both detritus and plankton. The effects of these species on kelp forest dynamics can be substantial and are not limited to trophic attributes of the community. For example, in southern Californian forests, dense aggregations of the reef building bivalve, *Chama arcana*, and the vermetid gastropod, *Serpulorbis squamigerus*, enhance the structural heterogeneity of rocky reef surfaces. Similarly, gorgonians and the sea cucumber *Pacythyone rubra* can carpet reef surfaces to the exclusion of other sessile species, including habitat-forming macroalgae like giant kelp (Patton et al. 1995).

Grazers and detritivores

The great productivity of erect frondose algae on shallow subtidal reefs also supports a high diversity of herbivorous grazers. However, most grazers, perhaps with the exception of a few herbivorous fishes, also utilize detritus, including a variety of echinoderms (sea urchins, sea cucumbers, sea stars; Harrold and Pearse 1987), gastropods (Watanabe 1984, Schmitt 1985), and crustaceans (isopods, amphipods, shrimps, hermit crabs and spider crabs; Hines 1982, Coyer 1985). One clear example of differences in grazer composition between southern and central Californian kelp forests is the greater diversity of sea urchins in the South. Three species, *Strongylocentrotus pupuratus*, *S. franciscanus*, and *Lytechinus anamesus*, occur in particularly high densities in southern Californian forests and *Centrostephanus coronatus* is found only south of Point Conception (e.g., Harrold and Pearse 1987). Similarly, several predominant gastropod taxa such as *Lithopoma*, *Norrisia,* and (historically) several abalone (*Haliotis*) species are in greater abundance in southern Californian forests (Tucker 1954, Keen and Coan 1974). The seastar, *Asterina miniata*, is a prominent and ubiquitous detritivore-grazer in kelp forests throughout southern and central California (references in Leonard 1994). Like the planktivorous fishes mentioned above, the most abundant herbivorous reef fishes, the halfmoon, *Medialuna californiensis,* and the opaleye, *Girella nigricans*, are members of tropically-derived families (kyphosidae and girellidae, respectively) and are far more abundant south of Point Conception.

Primary predators

A suite of carnivorous fishes, gastropods, crustaceans and sea stars exploits this multitude of grazers and planktivores. Small reef fishes, including gobies, blennies, and especially the kelp fishes (family Clinidae), forage on the many small herbivorous crustaceans (for example amphipods) associated with macroalgae, as do larger reef fishes (for example surfperches, painted and kelp greenlings). Likewise, a number of carnivorous neogastropods feed on barnacles and other sessile invertebrates. The predatory gastropods, especially of the family Muricidae, as well as whelks (e.g., *Kelletia*) and cowries (e.g., *Cyprea)* are diverse and abundant in southern Californian forests. Particularly voracious and abundant predators are the many sea stars that, like their intertidal counterparts, are responsible for creating and maintaining a patchy distribution of the benthic sessile fauna and for producing rocky surfaces available (and highly contested) for settlement and recruitment of sessile species (Duggins 1983, Harrold and Pearse 1987). Due to their high mobility, large sea stars (such as the sunflower star, *Pycnopodia helianthoides*) also influence the local abundance of mobile grazers, particularly gastropods (Watanabe 1984) and sea urchins (Duggins 1983, Harrold and Pearse 1987). Because of the greater diversity and abundance of sea stars with increasing latitude, their role in kelp forest food webs seems to increase in more northerly forests, a pattern amplified by the fact that sea star populations in southern California have also experienced episodic disease outbreaks (Tegner and Dayton 1987). Octopi are also voracious gastropod predators in kelp forests throughout California, but especially so in southern California (Rosenthal et al. 1974, Pearse and Hines 1976, Ambrose 1986). Predation by the largest crustaceans in the system, cancer crabs and the California spiny lobster (*Panulirus interruptus*), rivals that of sea stars and octopi. Indeed, one of the most conspicuous differences in the regime of primary predators between southern and central kelp forests is that *P. interruptus*, which preys upon bivalves, gastropods and sea urchins (Mitchell et al. 1969, Tegner and Levin 1983, Robles 1987), occurs only south of Point Conception, where it is abundant.

Secondary predators

Kelp-forest planktivores, detritivores, grazers, and primary predators are eaten by fishes, birds (including cormorants, herons, egrets), marine mammals (seals, sea lions, sea otters), and humans. Kelp-forest secondary predators constitute three feeding groups: species that primarily consume (1) fishes, (2) invertebrates, or (3) both fishes and invertebrates. Of the species that feed primarily on fishes, both birds and marine mammals are substantial sources of predation in both southern and central Californian forests (Foster and Schiel 1985). Whether or how the magnitude of predation by these groups varies regionally is not clear, especially because of the great spatial variation in their distribution and foraging activities within each region. For most kelp-forest fishes, however, the major source of mortality is predation by piscivorous fishes, reflected by both the massive mortality of the small juvenile stages that are vulnerable to predation by larger fishes and the predominance of small fishes in the diet of many piscivorous fishes (reviewed by Steele and Anderson 2005, Carr and Syms 2005).

Given the differences in the representation of tropical and temperate families in central and southern kelp forests, it is not surprising that species composition of piscivores varies regionally. For example, the piscivorous sea basses (especially the kelp bass) are prevalent predators in the south (Limbaugh 1955, Young 1963, Quast 1968a) and the rockfishes (genus *Sebastes*) are the most prevalent piscivores in the north (Hallacher and Roberts 1985). There are also conspicuous regional differences in species composition for invertebrate predators. Sea otters (*Enhydra lutris*) were extirpated from southern California in the early 1800's and have yet to permanently recolonize regions south of Point Conception (Riedman and Estes 1988), but they appear to play a particularly important role in limiting the density of the dominant herbivores, such as sea urchins, in central Californian forests (articles reviewed by Harrold and Pearse 1987, Ebeling and Laur 1988, Estes and Harrold 1988). In southern Californian forests, their role is replaced in part by one fish, the California sheephead (Cowen 1983, 1986), and possibly a crustacean, the California spiny lobster, *Panulirus interruptus* (Tegner and Levin 1983, Lafferty 2004). These regional taxonomic differences, combined with regional differences in the relative productivity of both frondose algae and plankton, set the stage for marked differences in key species interactions that both establish and maintain the structure of kelp forests in central and southern California.

Food Web Structure

One property clearly common to southern and central Californian kelp forests is the fundamental importance of kelp (primarily *Macrocystis pyrifera*) as an overwhelming source of primary production and detritus that fuels both the grazer-dependent and the detritus-dependent trophic pathways in these systems (Fig. 3). The actual diversity of forest-dwelling species involved in either or both of these pathways has never been quantified, but clearly constitutes a major portion of the great diversity characteristic of these communities (Graham 2004). Thus, one consideration for increasing our understanding of the ecological processes that fundamentally structure Californian kelp forest communities is to determine how these systems change in response to variation in the presence or abundance of kelp.

It is obvious that localized kelp loss will have ecological consequences, since remaining non-kelp primary producers cannot replace the vast amounts of energy and habitat lost. But for any given system it is unknown whether the changes will come in terms of species biomass (including habitat structure), productivity, or diversity. The inability of ecologists to predict such tangible consequences of kelp loss is due largely to our inability to isolate trophic from habitat linkages between kelp and their associated species, and to distinguish them from other species interactions or associations. For example, in Californian *Macrocystis* forests some generalist taxa, such as sea urchins, receive the bulk of their energy from giant kelp drift when it is present (Pearse and Hines 1976, Harrold and Reed 1985), suggesting a strong trophic linkage. Nonetheless, sea urchins can survive for years to decades in the almost complete absence of large attached macroalgae (Harrold and Pearse 1987); the abundance of abalones, however, appears to be more dependent on a constant source of drift kelp as abalone are lost from some southern Californian systems following episodic deforestation (Graham 2004).

Habitat linkages may be just as problematic since some taxa, such as kelp surf perch (*Brachyistius frenatus*) and the kelp goby (*Lethops connectens*), appear to have essentially obligate associations with giant kelp structure at some stage in their life history (Graham 2004), whereas others, such as Norris's top snail (*Norrisia norrisi*), giant kelp fish (*Heterostichus rostratus*), kelp bass (*Paralabrax clathratus*), kelp rockfish (*Sebastes atrovirens*), and juveniles of several species of rockfishes, have only facultative relationships with the forest structure, often associating with various algae that are either present as an understory beneath sparse canopies or continuing to exist in the complete absence of kelp forests; yet all of these species respond negatively to giant kelp removal (Miller and Geibel 1973, Bodkin 1988, Ebeling and Laur 1988, Carr 1989, 1991, 1994, DeMartini and Roberts 1990, Holbrook et al. 1990, Anderson 1994, Graham 2004, Stephens et al. 2005). The job of disentangling trophic from habitat associations seems daunting given that many taxa have both trophic and habitat linkages, omnivory is poorly understood, and the importance of indirect interactions in a community with >200 common species (Graham 2004) is unknown.

No studies have addressed variability in the strength of trophic links in kelp forests across any temporal or spatial scale, although Sala and Graham (2002) did study among-species variability in interaction strength between *Macrocystis pyrifera* and its invertebrate grazers. Still, the last 50 years of ecological and natural history studies suggest that differences in the strength of trophic links exist between southern and central Californian forests. Some planktivores are noticeably more abundant in southern than in central Californian forests (for example the blacksmith, a very abundant planktivorous damselfish; Hobson and Chess 1976, Ebeling et al. 1980, Bray 1981), but great concentrations of zooplankton in the coastal waters of central California support large standing biomasses of several species of planktivorous juvenile and adult rockfishes (genus *Sebastes*; Hallacher and Roberts 1985, Singer 1985, Gaines and Roughgarden 1987, Carr 1991). Many species of fish have juveniles that are numerous, planktivorous, and co-occur in both regions (for example senoritas and kelp perch). High biomasses of planktivores in central Californian forests may reflect the greater coastal productivity in the upwelling-dominated ocean climate that characterizes inshore waters north of Point Conception (Strub and James 2000).

A second interesting property of Californian kelp forest food webs is that, despite the relatively high species richness of the kelp forest communities, few primary consumer taxa, such as sea urchins or amphipods, have been shown to overexploit producer populations. Furthermore, although abiotic factors can be key in controlling grazer outbreaks (see Ebeling at al. 1985, Foster and Schiel 1988), when predation is found to be important, only a small set of upper-level predators is apparently necessary to control these grazer populations. Sea otters are voracious predators of sea urchins, but in California they are restricted primarily to kelp forests north of Point Conception (Riedman and Estes 1988). The effect of sea otters in central California may be reinforced by the greater abundance of two other sea-urchin predators that become increasingly abundant from south to north: the predatory sea star, *Pycnopodia helianthoides* (Duggins 1983), and the wolf eel, *Anarrichthyes occellatus* (Hulberg and Graber 1980). In the absence of this suite of predators in southern California, the spiny lobster (*Panulirus interruptus*) and the California sheephead (*Semicossyphus pulcher*) have been identified as potential sea-urchin predators. Large sea urchins may, however, have a size-refuge (Cowen 1983, Tegner and Levin 1983, Cowen 1986, Lafferty 2004). Changes in sea urchin densities in response to either experimentally altered sheephead densities (Cowen 1983) or differences in lobster densities inside and outside marine reserves (Lafferty 2004) are consistent with the influential role of these two species in forests along the Californian Channel Islands. The southern Californian kelp forest has maintained a sea urchin fishery due to lower levels of natural predation in the absence of the sea otter. Finally, another key regional difference between these systems is that upper-level predators, such as lobster and sheephead, are heavily targeted by fisheries in southern California while sea otters are protected in central California.

The potential for overgrazing is not only regulated by predation. The strength of interactions between grazers and giant kelp forests in southern and central California may also reflect differences in the balance between kelp productivity and herbivory between these regions. In central California, no observations of overgrazing of *Macrocystis pyrifera* by the highly abundant herbivorous crustaceans that inhabit and graze giant kelp plants have been recorded. In contrast, observations of herbivory by the amphipod, *Amphithoe humeralis*, leading to massive kelp biomass loss, have been recorded in southern Californian forests (Tegner and Dayton 1987, Dayton et al. 1998, Graham 2002). The ability of these small, abundant grazers to cause marked declines in forest biomass may reflect (1) a lower productivity potential of southern Californian kelps, (2) greater vulnerability of primary producers (kelps) to oceanographic variability in southern California (e.g., ENSO), or (3) greater effects of such oceanographic variability in southern California on the abundance of primary predators that may control grazers (negative effects of ENSO on planktivorous fishes that control amphipod outbreaks; Tegner and Dayton 1987, Dayton et al. 1998, Graham 2002). Thus, the strength and effect of trophic interactions may vary regionally in response to large-scale variation in oceanographic processes that influence either producer or consumer populations, or both.

Temporal and Within-region Spatial Variation

Food Web Dynamics and Productivity

Southern and central Californian kelp forests share one fundamental trait: the reliance on large kelps as the primary source of energy and biogenic habitat. Still, large regional differences exist in species composition and the identity of key species, both of which appear to be due in a large part to broad-scale biogeographical processes. Within regions, however, the dynamics and productivity of kelp populations can also be highly variable in space and time. For example, the dynamics of perennial *Macrocystis pyrifera* populations on either side of the Monterey Peninsula (Hopkins Marine Station vs. Stillwater Cove) can be out of phase despite being separated by only 15 kms of coastline; this pattern appears to be due to both variable exposure to ocean swell (northwest swell vs. southwest swells, respectively) and the rock type of the reefs (see similar arguments by Foster and Schiel 1985, 1988). Four kms south of the Monterey Peninsula along the central Californian coast, energy input to kelp forest systems is likely constrained by the restricted productivity of the annual kelp *Nereocystis luetkeana*, which can dominate the exposed open coastline (Foster and Schiel 1985). Finally, there appears to be little coherence to the dynamics of local *Macrocystis pyrifera* populations south of Point Conception, even those at opposite ends of the same kelp forest (Dayton et al. 1992, 1999), except during catastrophic ENSO events when most southern Californian kelp forests are simultaneously decimated (Edwards 2004).

Nearshore oceanographic processes can be important in regulating various aspects of the population biology of kelp forest species, including dispersal, nutrition, reproductive output, and survival, and thus environmental factors can directly cause fluctuations in kelp forest producer and consumer populations. Indeed, each kelp forest species must be considered to have a component of its population variance due to processes unrelated to associations with kelps. Well documented within-region variability in kelp population dynamics (Dayton et al. 1992, 1999) and known trophic and habitat associations among kelp forest species suggest, however, that kelp-associated processes may be responsible for much of the food-web dynamics over short spatial scales and a broad range of temporal scales. Furthermore, kelp-forest species may have trophic and habitat associations with particular kelp taxa, such as canopy-fishes obligatorily associated with *Macrocystis pyrifera* (Graham 2004). Although the extent of associations with particular kelp taxa have yet to be explored, geological and oceanographic processes that regulate the distribution and abundance of specific kelp taxa may also have important effects on the structure and dynamics of kelp forest food webs. In the next section, we discuss various methodological and theoretical challenges of disentangling the roles of trophic interactions from habitat associations in structuring kelp forest communities.

Ecological Consequences of Kelp Loss

Despite known trophic and habitat associations among kelp forest taxa, the inherent complexity of these communities makes it difficult to study community responses to continuous variability in kelp distribution and abundance. The approach of directly relating species abundance to kelp abundance (such as kelp frond density or biomass/m^2) has only proven feasible when working with small groups of closely-associated taxa (Holbrook et al. 1990). Consequently, community-based studies would be most beneficial if designed initially to focus attention on community responses to kelp loss (i.e. presence vs. absence of kelp; Graham 2004) at a variety of temporal and spatial scales, and some researchers have directly studied the effects of kelp loss on specific assemblages within kelp forest communities (Reed and Foster 1984, Clark et al. 2004).

Experimentally-based studies, and large-scale long-term observational studies may be useful for studying the effects of kelp loss on community structure and food web dynamics. Specifically, experiments are useful for disentangling the many potentially confounding influences of processes that co-vary among and within forests over time, including kelp canopy biomass and detrital production, and to identify the causal relationships between components of the system. Monitoring studies, on the other hand, can reveal the strength of relationships between different community components across broad temporal and spatial scales, and help to define a broader context for interpreting conclusions drawn from more restricted experimental studies. Here, we introduce a series of experiments designed to disentangle trophic interactions from habitat associations, and argue for a broader role of large-scale, long-term monitoring studies of environmental correlates.

Experimental protocols

One of the most exciting characteristics of kelp forest communities is that they are inherently amenable to experimental manipulations. Given their sessile habit, the distribution, abundance and size of individual kelp plants and populations can be manipulated over ecologically relevant temporal scales of weeks to generations (Ambrose and Nelson 1982, Ebeling and Laur 1985, Bodkin 1988, Eckman et al. 1989, Carr 1989, 1994, Reed 1990, Dayton et al. 1999, and Clark et al. 2004). Many questions await field experimentation: (1) What are the relative contributions of kelp production and habitat provision to kelp forest community structure? (2) To what extent does alteration of the physical environment by kelp, such as subsurface light, sedimentation, water motion, and turbulence, confound the provision of energy and habitat? (3) Is the positive effect of kelp presence on community function restricted to particular kelp taxa? (4) If so, what biological characteristics of these taxa are responsible for the effect? (5) What are the relative contributions of direct grazing vs. phyto-detritus production to secondary production (i.e. consumer production)? (6) How much variability in kelp forest dynamics and diversity can be accounted for by the effect of kelp on other energy and habitat providers, such as understory algae? (7) What are the relative contributions of phytoplankton versus frondose algal primary production?

Although broad in scope, each of these questions can be addressed either directly with manipulation of various components of local kelp stands, (such as entire plants, canopy biomass, detritus, turf algae abundance, kelp species composition) or in combination with ecological modelling (e.g. ECOPATH), trophic analyses (e.g. stoichiometry), and laboratory studies of species interactions (Anderson 2001). In theory, the design of such experiments is straight-forward, and indeed each of these components has been manipulated to some extent by past researchers. The key for community-level studies, however, is to conduct the experiments over a broad enough range of spatial and temporal scales to ensure independence of treatment levels and relevance to entire kelp forest communities.

The mobility of many temperate species, especially fishes, and the slow growth and demographic responses of the many long-lived species necessitate large scale, long-term press manipulations to assess the community-wide influence of kelp. Optimal experimental designs would include replicates of independent reefs with randomly allocated kelp treatments (no kelp vs. kelp with canopy, vs. kelp without canopy). The large size of most natural reefs along the Californian coast, however, makes this logistically problematic. Alternatively, large-scale removal of kelp (100's of meters) between replicates within a large continuous kelp forest could be used to create independent kelp treatments. In either case, water motion, import/export of phytodetritus, and immigration and emigration of consumers are likely to interact with kelp populations at scales >100 m (Jackson and Winant 1983, Jackson 1998), and thus efforts to expand the scale of such manipulations are critical to the advancement of our understanding of these systems. Furthermore, decoupling the relative effects of primary production and habitat structure on a forest's influence on community structure would entail artificial kelp structures akin to similar approaches used in seagrass systems (Bell et al. 1985), but at a more grand scale. Probably the most tractable experiments are those that directly manipulate kelp species composition, canopy structure (i.e. biomass), standing-stock of large phytodetritus (drift kelp), and grazer abundance. Because removal of kelp abundance simultaneously alters the energy source and the physical structure, decoupling of the two processes can only be achieved by holding one constant while removing the other. For example, with canopy removals, artificial kelp can be added to mimic physical structure and drift kelp can be added or removed to manipulate an energy source, although it is unknown how well manipulations of phytodetritus can be maintained in such fluid habitats. We consider that persistent removal of kelp canopy and phytodetritus, perhaps orthogonally to ascertain their relative and combined effects, may be feasible over reasonable spatial scales.

Role of long-term time series

How do the structure and dynamics of kelp forest communities vary in relation to local and regional differences in geologic (substratum type and relief) and oceanographic (wave exposure, oceanic productivity) attributes? How does the inherent richness of a region (biogeography) affect the role of kelps in the system? What is the role of episodic oceanographic events (ENSO) or regime shifts in regulating kelp-consumer associations? What are the relative contributions of nutrients from terrestrial and oceanic sources to kelp plant productivity and its utilization by kelp forest communities? The answers to such questions are vital to our understanding of the function of kelp systems, yet these processes vary over broad enough scales to be outside the range of field experimentation. As such, future studies will need to complement field experimentation with long-term monitoring of key kelp forest attributes such as kelp distribution and biomass, abundances of important consumer, environmental parameters and to incorporate techniques not regularly utilized by kelp ecologists, including numerical modelling, genomics, stoichiometry, palaeontology, and archaeology.

In California, some organizations are collecting relevant ecological data on kelp forest community structure over broad temporal and spatial scales, for example the Channel Islands National Park kelp-forest monitoring program or the Partnership for Interdisciplinary Study of the Coastal Oceans (PISCO). These programs provide invaluable data to broaden the interpretation of small-scale field experiments that are replicated over broad spatial scales. Furthermore, numerous local, regional, state, and federal institutions and agencies are collecting long-term data sets of key parameters of particular species useful for long-term studies of kelp forest systems. For example, aerial photographs of kelp canopy area have been collected by various people and groups over many regions in California for the last 60 years, and have supported numerous ecological studies of kelp systems; such long-term monitoring of kelp canopies has been greatly enhanced by regular aerial surveys using digital photography and multi-spectral data collection. Hyperspectral surveys conducted by the Center for Integrative Coastal Observation Research and Education (CI-CORE) offers promise for remote sensing of specific kelp species, and even health and productivity of kelp canopies.

One new and exciting approach to understanding long-term change in kelp forest community structure is to explore the geologic and palaeontological records of human use of kelp forest resources to reconstruct the spatial chronology of forests within and between regions (Graham et al. 2003, Kinlan et al. in press). In California, archaeological collections from human midden sites on the Channel Islands and southern and central Californian mainland include rich marine invertebrate and vertebrate assemblages extending back almost 13,000 years (Erlandson et al. in press). In addition to providing simple estimates of the abundance of abalone, sea urchins, gastropods, bivalves, fishes and mammals, many remains have a high level of organic matter preservation, which can lead to subsequent stable isotope and genetic analyses useful for the reconstruction of consumer diet and historical population size. Although such cross-disciplinary studies are rare for kelp systems, new technological advances, analytical tools, and a wealth of archived data provide numerous opportunities for cross-disciplinary explorations.

Human Influences

Aside from the regional extirpation of sea otters through the fur trade, anthropogenic disturbance to Californian kelp forest communities prior to 1900 came primarily from localized subsistence-level fishing. In the past century, however, and particularly in the past few decades, kelp communities have begun to experience dramatic increases in local and regional-scale pressure. These pressures include the entrainment of propagules (i.e. spores, eggs, larvae) by water intake systems, thermal pollution, increased turbidity and sedimentation associated with cooling waters of coastal power plants; commercial and recreational fishing; and regional to global-scale pressure from climate change. These shifts in the nature and the scale of human disturbance to kelp forest communities require new approaches for management and conservation. Some of these approaches are being implemented and are showing positive effects (for example establishment of Marine Protected Areas); other threats remain poorly addressed. Our focus here is to briefly discuss the potential causes of anthropogenic modification of kelp forest systems and its consequences for kelp populations.

Exploitation and Habitat Loss

The greatest direct impact to Californian kelp forest communities has come from human exploitation of mammals, fish, invertebrates, and kelp that make up these communities. Although this exploitation has been occurring for centuries, the rate and magnitude have increased significantly in the past few decades with the advent of new fisheries and new harvest methods. sheephead (*Semicossyphus pulcher*), lobsters (*Panulirus interruptus*), abalone (*Haliotis* spp.), and many rockfishes (*Sebastes* spp.) have all been over-fished, some to ecological extinction (Dayton et al 1998, Lafferty 2004), and in their place new fisheries on other rockfishes, sea cucumbers (*Parastichopus* spp.), sea urchins (*Strongylocentrotus* spp.), and sportfish like kelp bass (*Paralabrax clathratus*) have developed and are increasing.

These fisheries extract huge amounts of biomass from kelp forest ecosystems annually (Leet et al. 2001). Although not exclusively from kelp forests, commercial landings in California over the last decade (1994-2003) have averaged 187,870 metric tons (data from PacFIN), even with large spatial and temporal closures to groundfish, rockfish, and other species during this time period. Recreational fisheries have removed an average of 10,000 fish per year from Californian waters over this same time period, nearly a quarter of which were rockfishes (data from RecFIN). These recreational fisheries catches are much smaller than the commercial catches, but often target different species, particularly those that reside in kelp forests, and may thus affect kelp forest ecosystems disproportionately.

Many of these fished species are long-lived and slow-growing abalone and rockfishes, and may not be able to recover quickly from heavy fishing pressure. Past changes in fishing regulations for some of these species have had mixed results in maintaining sustainable population levels, leading to complete closure of the fishery in some cases. The great reduction in these kelp forest species is not trivial (Dayton et al. 1998); the structure of these biological communities has fundamentally changed. Evidence suggests that the dramatic reduction in the population sizes of species like lobsters, sheephead, and sea otters may have driven some kelp forests to become sea urchin barrens (Tegner and Dayton 2000, Lafferty 2004, Behrens and Lafferty in review). Because of the relatively slow growth of many sea urchin predators, the reversal of such community state shifts may take a decade or more even if fishing were to cease completely (Shears and Babcock 2003). Still, despite most of the southern Californian kelp forests lacking sizable populations of these predators, the forests *have not* collapsed (Steneck et al. 2002); Foster and Schiel (1988) alternatively suggest that physical processes affecting sea urchin mortality and recruitment, rather than predation, control sea urchin population explosions in California.

Giant kelp, *Macrocystis pyrifera*, has also been harvested for decades for use in a wide variety of food, cosmetic, and fertilizer products. Although this harvest appears to have little if any effect on the kelp (Kimura and Foster 1984), since kelps have extremely rapid growth rates (North 1994), not much is known about how kelp harvesting may affect the species that use kelp canopy as habitat. In particular, many rockfish (*Sebastes* spp.), kelp bass (*Paralabrax clathratus*), kelp surfperch (*Brachyistius frenatus*) and other species of fish are known to use the canopy as a nursery habitat. A few studies have examined the effects of kelp harvesting on associated fish populations or, in particular, the removal of kelp canopy as nursery habitat (Limbaugh 1955, Davies 1968, Quast 1968d, Miller and Geibel 1973). Most of these studies have been conducted in southern California and all have been limited in spatial scale or replication. It remains unknown how the timing or extent of kelp harvest influences post-settlement survival or the population dynamics of most fish species.

There is evidence that coastal pollution (Swartz et al. 1983), power plant operations (Schroeter et al 1993, Reitzel et al. 1994, Bence et al. 1996, Schiel et al 2004) and the dredging of channels and harbours (North and Schaefer 1964) also negatively impact kelp forest distribution. Although smaller in scale than the fishing effects described above, habitat loss and pollution have dramatically reduced the size of local kelp forests and the abundances of the associated biological communities (North 1971, Dayton et al. 1984, Schroeter et al 1993, Reitzel et al. 1994, Bence et al. 1996, Schiel et al. 2004); the effect of episodic oil spills on Californian kelp systems has been relatively minor (Foster et al. 1971). As humans continue to migrate to coastal areas, this pressure will certainly increase, although the effects can sometimes be counter-intuitive. For example, the large sewage spill that occurred in the Point Loma kelp forest actually benefited kelp populations by stimulating recruitment through nutrient input (Tegner et al. 1995).

Invasive species

The spread of non-native species into habitats and locations continues to be a global problem, yet the potential effect of invasive species on kelp forest systems is largely unknown. For example, *Sargassum muticum* has spread throughout the Northeast Pacific and persisted for many decades (Druehl 1973, Norton 1981). Its ability to rapidly colonize and cover completely canopy-free areas can prevent the re-establishment of giant kelp forests (Ambrose and Nelson 1982), although these effects appear to be limited in time and space (Foster and Schiel 1992). Two species of invasive seaweeds have only recently been introduced to California: the siphoneous green alga *Caulerpa taxifolia* (Williams and Grosholz 2002) and the Asiatic kelp, *Undaria pinnatifida* (Silva et al. 2002, Thornber et al. 2004). In California, neither species has been reported on natural substratum along the open coast, but both species have been documented to alter benthic community structure in other regions of the world where they have become abundant (Piazzi et al. 2001, Valentine and Johnson 2003, Casas et al. 2004). In the cases where *Undaria* has had an impact on natural kelp populations in Tasmania and Argentina, the inherent richness of the local kelp assemblages are an order of magnitude lower than in California (Valentine and Johnson 2003, Casas et al. 2004). It remains to be seen whether the increased diversity of Californian kelp forests can buffer them from the ecological and economic threats of invasion.

Climate Change

Changes in global and regional climate regimes are expected to affect Californian kelp-forest communities. Kelp have limited depth and temperature ranges; as sea level and surface temperature (SST) rise with global warming, kelp distributions will be modified according to subsequent changes in substrate distribution (rocky reefs) and productivity regimes amenable for kelp attachment and growth. For example, Holocene sea level rise likely led to large changes in total area of kelp forest habitat around the Californian Channel Islands as broad nearshore rocky platforms shrank (Graham et al. 2003, Kinlan et al. in press). This shift coincided with conspicuous changes in total biomass of kelp-associated species, such as abalone, sea urchins, and turban snails in Native American shell middens on the Channel Islands (Erlandson et al. in press). Similarly, past annual and decadal shifts in regional oceanographic temperature regimes have shifted the southern range limit of kelp in baja California, Mexico over 100 kms to the north (Hernandez-Carmona et al. 1989). If global climate change continues to drive SST higher, the southern limit of kelp distributions is expected to move further north along the baja and southern Californian coasts, depending on the magnitude of change in SST.

Finally, it has been suggested that climate change may be increasing the frequency of ENSO events (Diaz et al. 2001), which can have deleterious effects on kelp forests due to short-term increases in both SST (i.e. decreases in nutrient concentrations) and the intensity and frequency of storms (Dayton and Tegner 1984, Dayton et al. 1999, Edwards 2004). The combined pressures on kelps of higher SST and disturbance frequency in the southern end of the range may drive kelp range limits further north than would be predicted from either factor alone. Recent models of regional-scale effects of climatic change suggest that changes in the temperature differential between land and sea will alter coastal wind fields leading to changes in the frequency, magnitude and location of coastal upwelling that fuels kelp productivity (Bakun 1990, Diffenbaugh et al. 2004).

Management and Intervention

Efforts to control and manage human effects on kelp forest communities have for the most part focused on moving sewage discharges offshore and managing fishing effort. Additionally, huge spatial and complete fisheries closures have recently been implemented in attempts to restore depleted groundfish, such as the rockfish fishery. In response to the potentially unsustainable way that nearshore fish stocks have traditionally been exploited, recent efforts have turned to marine protected areas (MPAs) including no-take marine reserves as tools to complement management and protect multiple species simultaneously. Marine reserves have been shown to increase population sizes and species diversity within reserves in kelp forests around the world (Edgar and Barrett 1999, Babcock et al. 1999, Halpern 2003), although the reserves are most beneficial to target species and the effects on populations outside reserve boundaries will vary depending on patterns of larval dispersal (Gaines et al. 2003, Shanks et al. 2003, Palumbi 2003) and species mobility (Chapman and Kramer 2000), among other factors. Reserves incorporating kelp forests may also provide protection from kelp harvest to species using the canopy as nursery habitat, although the nursery contribution of kelp to growth and survival of juveniles relative to other habitats, has yet to be clearly documented or quantified.

Although reserves are likely to be able to provide protection from extraction of entire suites of species at once, they will be unable to account for threats to kelp forest communities caused by climate change. In fact, it may be difficult if not impossible to stop climate-driven changes from occurring, and so management efforts will have to be designed to account for rather than protect from these changes. Unfortunately, few if any current efforts to manage or protect kelp forest communities are accounting for the potential effects of climate change on these communities. Long-term protection is likely to be most successful if marine reserves are placed and sized to account for shifting species ranges (both across latitudes and depths) in response to global climate change (Halpern and Kinlan, in review).

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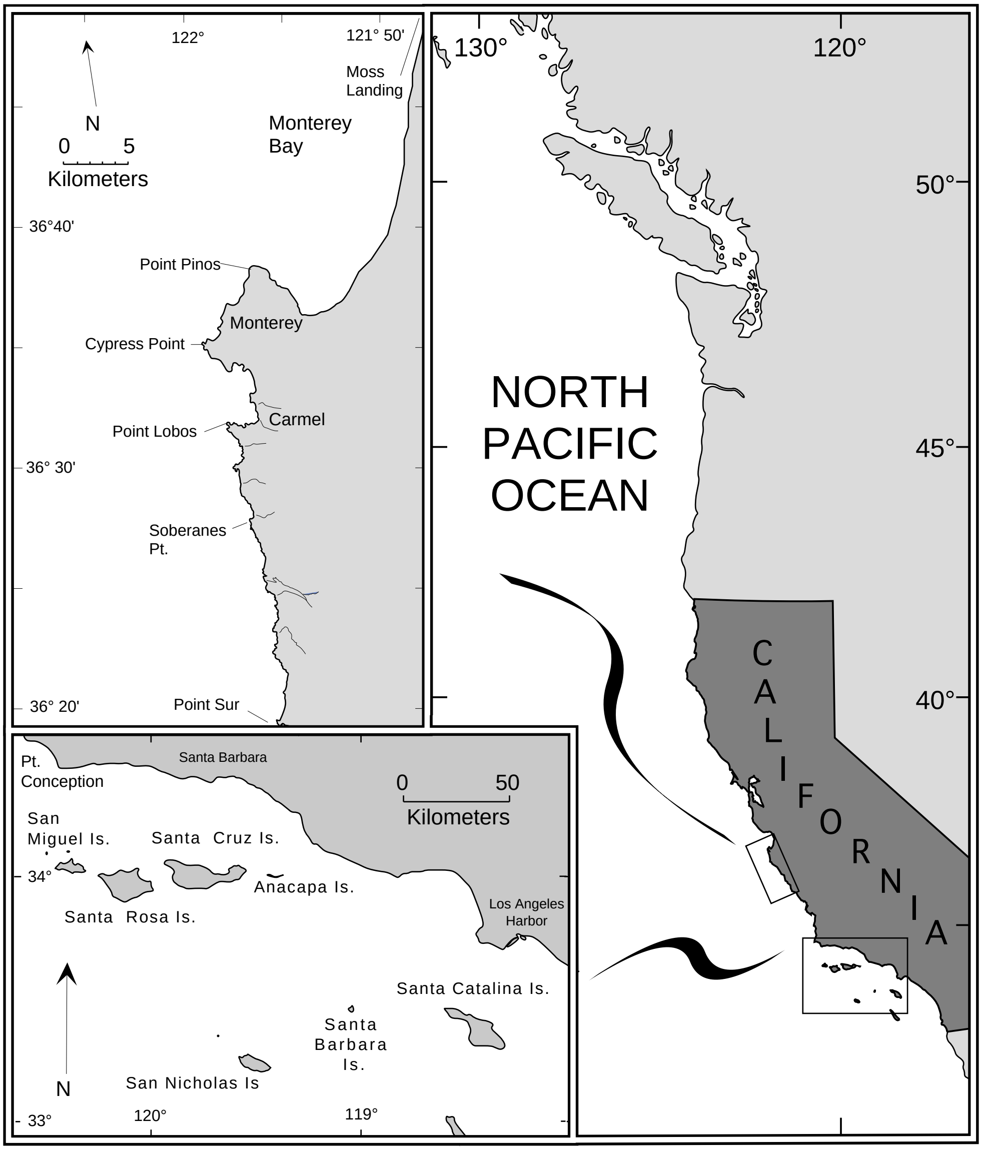
Figure Legends

Fig. 1. Location of central and southern Californian regions that include the kelp forests of primary focus in this paper. Point Conception marks the biogeographic transition point between the two regions, although the western Channel Islands (San Miguel and Santa Rosa) have fauna, flora, and oceanographic conditions similar to central California.

Fig. 2. Environmental conditions for the Monterey Bay and Channel Islands regions. Dark lines and points are mean values; bars indicate the range of possible values for that date (week or month) across all years data were available, except for chlorophyll and nitrate in Monterey where bars are 1SD. Temperature data come from 14 years of AHVVR satellite data (10x10km grid size; July 1985 – August 1999) and are 5-day averages of data from 10 grid cells each for the Monterey and Channel Islands regions. Significant wave height data are 5-day averages of hourly data from Buoy #46042 (Monterey; 1987-2002) and Buoy #46053 (Channel Islands, 1994-2002). Chlorophyll and nitrate data for Monterey Bay are from Mooring 1 (1990-2002); for the Channel Islands, the data are from CalCOFI tow stations 83.51, 83.42, 83.40.6, and 82.47 (1985-2002; means and ranges are calculated from all 4 tows).

Fig. 3. Californian kelp forest food web for both central and southern California. Trophic groups are indicated by dashed boxes, dominant taxonomic groups within the trophic group are indicated with solid-line boxes, and trophic links are shown with directional arrows.


122°
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Moss Landing
N
0 5
Kilometers
Monterey Bay
36°40'
Point Pinos
Monterey
Cypress Point
Carmel
Point Lobos
36° 30'
Soberanes Pt.
36° 20'
Point Sur
130°
120°
50°
45°
40°
NORTH PACIFIC OCEAN
CALIFORNIA
Pt. Conception
Santa Barbara
0 50
Kilometers
San Miguel Is.
Santa Cruz Is.
34°
Anacapa Is.
Santa Rosa Is.
Los Angeles Harbor
Santa Catalina Is.
Santa Barbara Is.
San Nicholas Is
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33°
120°
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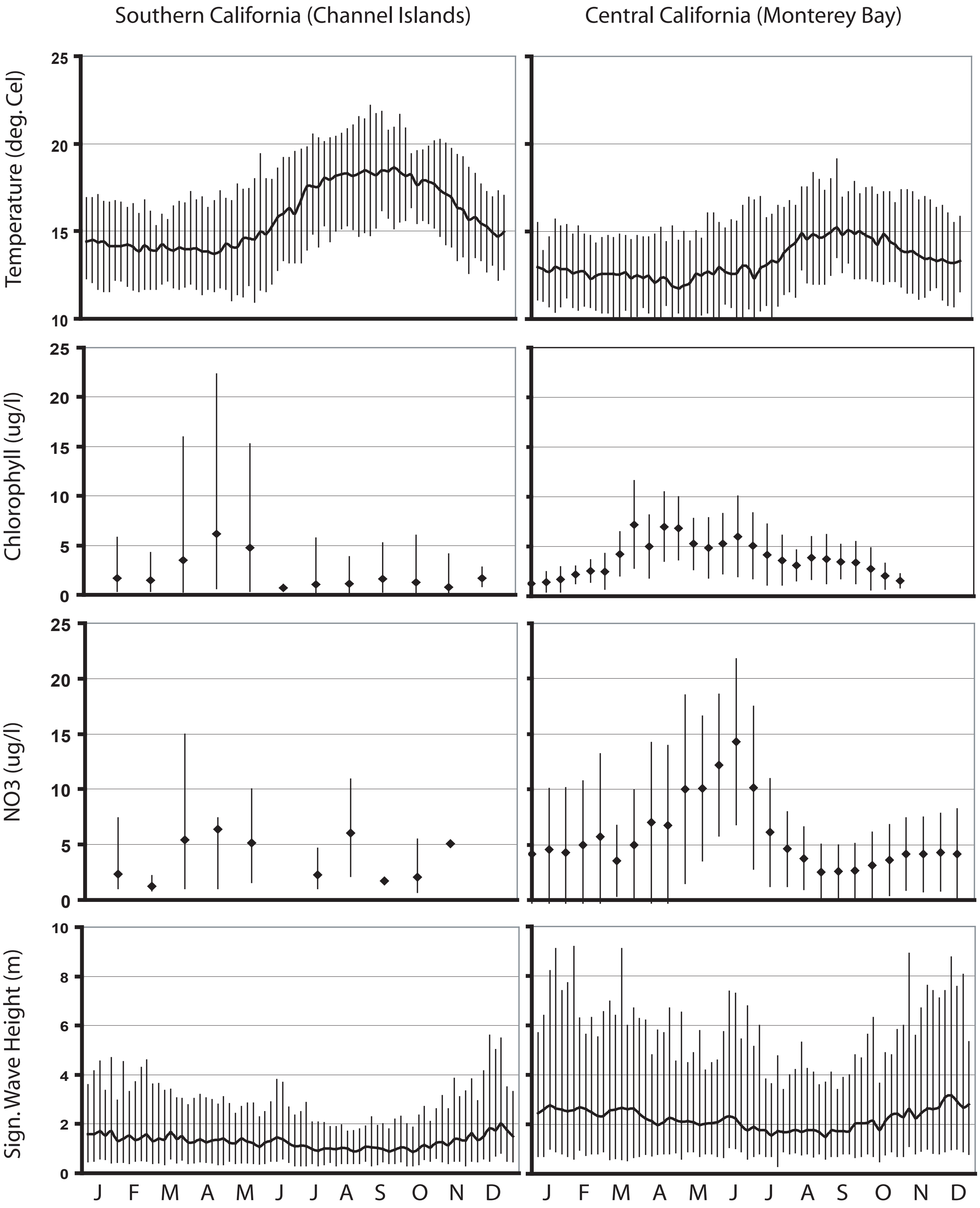

Southern California (Channel Islands)
Central California (Monterey Bay)
Temperature (deg. Cel)
25
20
15
10
Chlorophyll (ug/l)
25
20
15
10
5
0
NO3 (ug/l)
25
20
15
10
5
0
Sign. Wave Height (m)
10
8
6
4
2
0
J F M A M J J A S O N D
J F M A M J J A S O N D

California Kelp Forest Food Web