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Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs (in press: Ecosystems)

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Abstract

It has been hypothesized that the high diversity of giant kelp forests is due primarily to the provision of energy and habitat by the giant kelp (*Macrocystis pyrifera*). In this paper, I use a 19-year-long kelp forest monitoring data set from the Channel Islands National Park to (1) identify associations between subtidal species and forested or deforested habitats, (2) generate an idealized food web for southern California giant kelp forests in order to identify the primary conduits of energy flow through the system, and (3) determine changes in the diversity and complexity of this food web due to localized giant kelp deforestation. A total of 275 common species were observed in the Park between 1982 and 2000, of which 36% occurred significantly more often in kelp-forested areas than in deforested areas (i.e. sea urchin barrens); 25 species were found exclusively in forested areas. Most of these associations could be clearly identified as trophic and/or structural associations with giant kelp itself. The producer level of the food web was diverse, although giant kelp apparently represents the greatest single source of fixed carbon through either direct grazing or the production of phytodetritus. Primary, secondary and tertiary consumer levels were also represented by numerous species, and generalist consumers were common. With deforestation, the source of primary production shifts from primarily kelps to ephemeral micro- and macroalgae and phytoplankton. These results support the reliance of giant kelp forest food web structure and diversity on the presence of the forest itself.

Keywords: Giant kelp, *Macrocystis pyrifera*, kelp forests, deforestation, sea urchin barrens, habitat association, food web, foundation species.

Introduction

Forests of the giant kelp *Macrocystis pyrifera* sustain one of the most diverse, productive, and dynamic ecosystems on the planet (Mann 1973, Dayton 1985, Barnes and Hughes 1988, Graham et al. 2003). In southern California alone, over 200 species of algae, invertebrates, fishes, and mammals are commonly observed within giant kelp forests (North 1971, Foster and Schiel 1985), supporting a broad array of extractive and non-extractive industries including fisheries, aquaculture and tourism (Leet et al. 2001). The distributions of many of these organisms are known to be linked tightly to the presence of *M. pyrifera* due to a variety of trophic and habitat associations (see examples in North 1971, Foster and Schiel 1985). This integral role of *M. pyrifera* as the foundation of its associated community is supported not only by the vast amount of energy it produces (Parker 1963, Towle and Pearse 1973, Gerard 1976, Jackson 1977, 1987) or the highly structured 3-dimensional habitats that it provides (Quast 1971a, Feder et al. 1974, Ebeling et al. 1980, Coyer 1985, 1987, Ambrose and Swarbrick 1989, Holbrook et al. 1990), but also by the considerable amounts of fixed carbon (drift kelp) retained within and exported from coastal giant kelp forests (reviewed in Graham et al. 2003).

Natural history studies have described numerous trophic and habitat associations among giant kelp forest taxa, yet most studies have relied solely on qualitative and/or casual observations. Furthermore, the most extensive quantification of energy flow through a giant kelp forest remains the dissertation research of Gerard (1976). A few researchers have constructed giant kelp forest food webs that focus on specific producer-consumer interactions within particular geographic regions (e.g. the Chilean invertebrate and fish assemblages studied by Castilla 1985 and Angel and Ojeda 2001, respectively) or even individual reefs (e.g. Rosenthal et al. 1974). A generalized version of the Rosenthal et al. (1974) giant kelp forest food web was

developed by Foster and Schiel (1985), which emphasized the fundamental role of algal production, primarily from *Macrocystis pyrifera*, in regulating energy flow through the system and highlighted the diversity of trophic interactions that could be expected within any given kelp forest.

Still, the hypothesis that the diversity of giant kelp forest communities is founded upon the provision of energy and habitat by Macrocystis pyrifera has not been tested, due primarily to the logistic, economic, and environmental costs of manipulating kelp abundance at sufficiently large scales. Natural localized kelp loss due to deforestation, however, can occur over a wide range of temporal and spatial scales driven by a variety of abiotic and biotic processes (e.g. episodic storms, El Nino-Southern Oscillation events, or herbivore overgrazing; Zimmerman and Robertson 1985, Zimmerman and Kremer 1986, Dayton et al. 1992, 1999, Graham et al. 1997, Edwards 2001, Steneck et al. 2002). Conspicuous population explosions of kelp forest primary consumers (particularly sea urchins) have been documented at various times and places in California, resulting in kelp deforestation at a variety of scales (reviewed by Leighton 1971, Lawrence 1975, Foster and Schiel 1988, Steneck et al. 2002; the first description in California was by North and Pearse 1970). Such deforestation events can wipe out entire M. pyrifera populations with concomitant decreases in the abundance of various associated algae and animals (see for example Tegner and Dayton 1981, 1987, Graham 2002). Deforestation events might therefore be viewed as natural *M. pyrifera* removal experiments, although the community consequences of localized kelp deforestation have not been quantified.

As part of this special feature, I was charged with developing a modern food web for southern California giant kelp forests and identifying the ecologically important trophic linkages. The ecology of this complex and dynamic system has been extensively studied (reviewed by North and Hubbs 1968, North 1971, 1994, Dayton 1985, and Foster and Schiel 1985, Harrold and Pearse 1987, Foster et al. 1991), although there has been little attempt to study species-level trophic interactions beyond simple 2-species predator-prey linkages (e.g. Schmitt 1982, Sala and Graham 2002). As such, there is not enough data to rigorously study community-wide patterns in energy flow and the strength of trophic interactions. Here I summarize what is known about trophic interactions within giant kelp forests and place this information within a traditional food web framework to provide a foundation upon which such studies can be built. Specifically, I use 19 years of species presence-absence data for both forested and deforested areas in the Channel Islands National Park, California, USA, to: (1) identify associations between subtidal species and forested or deforested habitats, (2) generate an idealized giant kelp forest food web for the region, and (3) determine changes in the diversity and complexity of this food web due to localized deforestation. This paper therefore represents the first quantification of the effects of deforestation on an entire kelp forest community.

The dataset

Within southern California, episodic, yet ephemeral, kelp deforestation due to sea urchin overgrazing has occurred within the Channel Islands National Park (CINP; Figure 1) since the onset of long-term kelp forest monitoring in 1982. The CINP kelp forest monitoring program was designed to measure the limits of normal variation in the kelp forest community and diagnose abnormal conditions with the hope of prescribing remedial action through management recommendations (Davis et al. 1996). The CINP is ~1000 km² and surrounds the 5 northernmost southern California Channel Islands (San Miguel, Santa Rosa, Santa Cruz, Anacapa and Santa Barbara). Sixteen permanent study sites have been established within the CINP (Figure 1), each

marked by a 100 m long transect along which extensive community profiles of macroscopic taxa were made twice annually. Surveys were conducted using quadrats, band transects, random point contacts, visual transects, and roving diver counts (Davis et al. 1996). Specifically: (1) the distribution of discrete benthic organisms was estimated at each station using 24 paired 1 m x 1 m quadrats, 40 continuous and adjacent 1m x 5m quadrats, and 24 paired 3 m x 10 m band transects that were systematically arranged along the transect; (2) the distribution of encrusting invertebrates and macroalgae was estimated using 600 non-adjacent points (point contacts) randomly distributed along each transect; (3) the distribution of fish and pinnipeds was estimated using four 2 m x 3 m x 50 m fixed visual transects and a timed roving diver count. A total of 716 taxa were observed during the 19 years of CINP kelp forest monitoring, of which only 275 species were common enough to be observed in >12 of the 119 surveys (10%); my analyses were limited to these 275 common species. The remaining 441 rare species were primarily pelagics, or flora and fauna more commonly found in the colder waters of central California, warmer waters of southern and Baja California, or intertidal habitats. In no case did the published literature indicate that any of the 441 rare species were ecologically important in this system.

Previous researchers have reviewed studies of diet, predator-prey interactions, and species abundance that describe basic giant kelp forest trophic interactions (North and Hubbs 1968, North 1971, 1994, Feder et al. 1974, Rosenthal et al. 1974, Morris et al. 1980, Castilla 1985, Dayton 1985, Foster and Schiel 1985, Harrold and Pearse 1987, Foster et al. 1991, Angel and Ojeda 2001, Hobson and Chess 2001). Based on these studies, taxa from the CINP surveys were organized into producer and primary, secondary and tertiary consumer levels. Taxonomic groupings ranged from species to functional groups and were coarse when groups contained many species of *putatively* similar trophic importance (e.g. sessile invertebrates). These

groupings were not based on feeding modes as in Foster and Schiel (1985), since many of the taxa can effectively utilize >1 mode. Due to broad diets, a few heterotrophic taxa were considered to belong to more than one consumer level (e.g. filter-feeders that eat macroalgal phytodetritus, phytoplankton, and zooplankton). These taxa were assigned to the lowest appropriate consumer level. Assignment of species to taxonomic groupings facilitated the clear presentation of species diversity data, but was primarily done to facilitate the food web analyses.

Given the variable nature of sea urchin grazing fronts, the CINP kelp forest monitoring program has witnessed both short- and long-term shifts between kelp forests and sea urchin barrens at many sites, resulting in taxonomic lists for both forested and deforested assemblages; sea urchin barrens are regions that are generally devoid of macroalgae except crustose corallines and are maintained in that state by sea urchin grazing (Harrold and Pearse 1987). In some cases, multiple transitions between forested and deforested states occurred within a given site. Each of 119 CINP surveys between 1982 and 2000 were determined to be either 'forested' (n = 65) or 'deforested' (n = 54) based on a discriminant function analysis of community structure data (Behrens and Lafferty unpublished manuscript); an additional 55 'transitional' surveys could not be classified as forested or deforested based on community data and were disregarded. The estimated accuracy of the discriminant function analysis was 97%.

I compared the frequency of occurrence of the 275 common species from the CINP surveys between forested and deforested areas to determine which species were habitat associated and which were not. I examined the frequency of occurrence of common taxa among forested and deforested surveys using a heterogeneity chi-square (χ^2) analysis: (1) χ^2 statistics comparing forested to deforested habitats were computed for each of the 275 common taxa (using Yates correction for 1 df contrasts); (2) all 275 statistics were ranked from low to high; (3)

a running cumulative heterogeneity χ^2 was estimated; and (4) the species occurring significantly more often in one habitat or the other were identified as those with cumulative heterogeneity χ^2 exceeding a critical value ($\chi^2 = 313.6$, df = 274, $\alpha = 0.05$). Significant species (i.e., species with cumulative $\chi^2 \ge 313.6$) were determined to be forest-associates or barrens-associates based on the habitat they were most commonly found, and non-significant species were labeled as 'ubiquitous', meaning that there was not enough data existed to detect a statistical association. I then combined the assignment of habitat association, with information from published studies of giant kelp forest trophic dynamics, to produce traditional food webs for forested and deforested areas.

Habitat associations

In total, 99 species were found to be associated with either forested or deforested habitats (Figure 2, Appendix 1A), whereas 176 species were found to be ubiquitous (Figure 3, Appendix 1B). All but 1 of the 99 habitat-associates were more commonly found in forested habitats. The only species found to be significantly more common in deforested habitats was the sea urchin *Lytechinus anamesus*; 77% of *L. anamesus* observations were in sea urchin barrens (Figure 2A). Consequently, the total reduction in species richness as the CINP sites shifted from forested to deforested states was 97 taxa out of 274 (i.e. 35%). Furthermore, 151 of the 176 ubiquitous species and 251 of the 275 total species observed in the CINP surveys were more common in forested areas (Figures 2 and 3).

Of the 98 common taxa identified as forest-associates, 25 were found exclusively in forested areas (Figure 2B). As might be expected, these taxa primarily included kelp and other foliose macroalgae that would have been removed directly by sea urchin grazing in deforested

areas. Some bryozoans, hydroids and sponges were also found to be forest-obligates, likely due directly to sea urchin foraging or indirectly to the removal of macroalgal substrates by sea urchin grazing. The obligate nature of associations for shiner surfperch *Cymatogastor aggregata* and the canopy-dwelling kelp crab *Pugettia producta* corresponded with their attraction to *Macrocystis pyrifera* canopies, whereas the umbrella crab *Cryptolithoides stichensis* was likely a forest-obligate due to its usage of foliose macroalgal and geniculate coralline habitats as cover.

Published natural history studies have described clear functional ties to the presence of macroalgae (and *Macrocystis pyrifera* in particular) for many of the 73 non-obligate forest-associates (Figure 2C). Both common abalones were found to be forest-associates, which is not surprising given their primary dependence on kelp phytodetritus for food (Leighton 1971). Numerous other forest-associates utilize kelp phytodetritus (e.g. sessile invertebrates) and may also be energetically reliant on this kelp subsidy. Although other studies have demonstrated that ingestion of macroalgal phytodetritus can significantly enhance the secondary production of filter feeders (Duggins et al. 1989), it is unknown whether any of the statistical associations of sessile species with forested habitats were due to trophic interactions. The encrusting bryozoan *Membranipora membranacea* is a ubiquitous epiphyte of giant kelp, and many of the other forest-associated sessile invertebrates commonly encrust kelps and macroalgae suggesting that their associations were likely structural. The forest-association of sessile invertebrates directly attached to rocks, however, is probably due to direct impacts of sea urchin movements than to the actual loss of macroalgae.

Numerous non-sessile primary, secondary and tertiary consumers were also identified as forest-associates, many of which had clear habitat or trophic associations (Figure 2C). Many of these were canopy-dwelling species that depend on water column habitat provided primarily by

Macrocystis pyrifera (see also Ambrose and Swarbrick 1989, Holbrook et al. 1990). For example, most field observations in the CINP (and elsewhere) of the gastropod *Norrisia norrisi*, the isopod *Idotea resecata*, and the carnivorous fishes *Brachyistius frenatus*, *Sebastes atrovirens* and *Heterostichus rostratus* occur within and around *M. pyrifera* canopies (e.g. Feder et al. 1974, Ebeling et al. 1980, Coyer 1985, Stebbins 1986, Anderson 1994, Hobson and Chess 2001); Holbrook et al. (1990) similarly observed significant increases in the density of *B. frenatus*, *S. atrovirens* and *H. rostratus* with increased *M. pyrifera* abundance. Many non-canopy species were also identified as forest-associates, including the harbor seal *Phoca vitulina*, the sea star *Pycnopodia helianthoides*, and the sheephead *Semicossyphus pulcher*, the latter two of which are generalist kelp forest predators, suggesting a trophic association. The forest-associated crab *Cancer antennarius* is commonly found around the base of kelp holdfasts (Morris et al. 1980) and may have a structural association with *M. pyrifera*. Many of the non-obligate forest associations appeared to be due primarily to the presence of *M. pyrifera* in forested areas.

On the other hand, forest-associations of the fishes *Embiotoca jacksoni*, *E. lateralis*, and *Gibbonsia elegans* were likely due to habitat modifications other than kelp loss. Specifically, Carr (1989) and Holbrook et al. (1990) found that the abundance of *E. jacksoni* was positively related to *M. pyrifera* abundance due to usage by the fish of the low-lying turf algae present beneath dense kelp canopies, whereas both *E. lateralis* and *G. elegans* declined with increased *M. pyrifera* abundance due to the negative effects of canopy shading on foliose algae, which serve as nursery and foraging habitats. The positive association between *E jacksoni*, *E. lateralis*, *G. elegans* and *M. pyrifera* in the CINP therefore was likely due to the direct removal of both foliose and turf algae by sea urchin grazing in deforested areas. No herbivorous fishes, sea

cucumbers, octopi, sharks and rays, or sea urchins (as expected) were found to be associated with kelp habitats.

Of the 176 ubiquitous species in the CINP (Figure 3), 13 were non-kelp macroalgae. However, aside from Laurencia pacifica, Dictyota binghamiae, the opportunist Colpomenia *peregrina*, and *Codium fragile*, no non-kelp macroalgal taxon was observed in more than 9 of the 54 deforested surveys, indicating that macroalgae in deforested areas were rare. Each of the sessile invertebrate taxonomic groupings contained ubiquitous taxa, although bryozoans, hydroids and sponges all had more forest-associates than ubiquitous taxa. Conversely, aside from abalones, all primary and secondary consumers were represented by more (often many more) ubiquitous taxa than forest-associates. That the two herbivorous fishes, Girella nigricans and *Medialuna californiensis*, were commonly found in deforested habitats suggested that they could either (1) feed on the remaining macroalgal assemblages, (2) shift diets more toward small invertebrates, or (3) move efficiently between forested and deforested areas. Previous studies have also highlighted a positive link between certain carnivorous fishes Damalichthys vacca, Paralabrax clathratus, Sebastes carnatus, S. caurinus, and S. serranoides and the presence of Macrocystis pyrifera (reviewed in Holbrook et al. 1990), yet all of these taxa were found to be ubiquitous and relatively common in CINP deforested areas (Figure 3).

The giant kelp forest food web

As expected, the producer base of the giant kelp food web for forested areas in the CINP was diverse (Figure 4A). Five kelp species represented the primary conduit of fixed carbon into the system. The competitive dominant, the canopy-forming kelp *Macrocystis pyrifera*, has the highest productivity and biomass per m² (reviewed by Foster and Schiel 1985, North 1994). The

other 4 kelps represented stipitate sub-canopy (*Eisenia arborea*, *Pterygophora californica*) and non-stipitate low-lying forms (*Dictyoneuropsis reticulata*, *Laminaria farlowii*). A highly diverse non-kelp macroalgal group was also present, represented by 38 common species of brown, green, and red algae (including geniculate coralline algae) and an understudied yet ubiquitous group of crustose (non-geniculate) coralline algae (presumably *Lithothamnion/Lithophyllum*). These kelp and non-kelp macroalgae support a detrital pool that represents a trophically important conduit of fixed carbon into the food web; *M. pyrifera* is generally the dominant contributor of macroalgalbased phytodetritus in this system (Zobell 1971, Gerard 1976, Harrold and Reed 1985).

Nine primary consumer groups were present in CINP forested areas (Figure 4A), which may seem surprising to those readers accustomed to the simple kelp-sea urchin-sea otter trophic cascade. Clearly, sea urchins can have an important and conspicuous role in modifying the structure of giant kelp forests (reviewed by Harrold and Pearse 1987), with large feeding aggregations of Strongylocentrotus franciscanus and S. purpuratus directly grazing all kelp and other macroalgae in their paths. Recall that sea urchin overgrazing putatively caused all of the deforestation events in the CINP. However, a number of other giant kelp forest primary consumers can have quantifiable impacts on primary producer abundance. Species of decorator and hermit crabs (e.g. Pugettia spp. and Pagurus sp.) and two species of herbivorous fishes (Girella nigricans and Medialuna californiensis) also feed on kelps and other macroalgae (Leighton 1971, Feder et al. 1974, Hobson and Chess 2001). Numerous herbivorous molluscs graze directly on kelp stipes, blades and their associated epibionts (e.g. Tegula spp. and Norrisia norrisi; Watanabe 1984a, Stebbins 1986, Coyer 1987, Wakefield and Murray 1998) or occupy the benthos and feed indiscriminately on macroalgal microscopic and small macroscopic stages (e.g. *Lithopoma* spp.; Leighton 1971). Surprisingly, except for *Idotea resecata*, small

crustaceans were not well represented by the CINP surveys, although these seemingly ubiquitous kelp forest consumers also directly graze the vegetative blades of adult kelp sporophytes and other macroalgae (Jones 1971, Coyer 1985, Graham 2002).

At least eight different primary consumer groups can also utilize the high abundance of algal phytodetritus present in giant kelp forests. Large pieces of drift represent the main source of energy to abalones and strongylocentrotid sea urchins (Leighton 1971) and can also be utilized by small gastropods (Schmitt 1982) and crustaceans (Jones 1971). Smaller pieces of drift represent the only apparent source of macroalgal production for a suite of sea cucumbers, brittle stars, zooplankton (e.g. mysids; Clarke 1971) and a diverse group of filter-feeding sessile invertebrates.

The food web for CINP forested areas included five secondary consumer groups all of which feed primarily on invertebrates (Figure 4A). Many species of sea stars, lobsters, crabs, and carnivorous mollusks prey upon sessile and slow moving mobile invertebrates (Mitchell et al. 1969, Rosenthal et al. 1974, Schmitt 1982, Tegner and Levin 1983, Watanabe 1984b, Robles 1987). Two species of octopus, *Octopus bimaculatus* and *O. rubescens*, feed on a few herbivore groups, but mostly on other predators (e.g. decapods, gastropods and carnivorous fishes; Rosenthal et al. 1974, Schmitt 1982, Ambrose 1984). Carnivorous fishes also exhibit a diverse array of trophic interactions in southern California kelp forests. Sheephead (*Semicossyphus pulcher*) feed on sea urchins, abalone, other gastropods, bivalves, crabs and sessile invertebrates (Quast 1971b, Feder et al. 1974, Cowen 1983, 1986, Hobson and Chess 2001). Señorita (*Oxyjulis californica*), kelpfish (*Gibbonsia elegans*, *Heterostichus rostratus*), kelp perch (*Brachyistius frenatus*) and juvenile rockfish (*Sebastes* spp.) feed on mysids, amphipods, isopods and kelp epibionts (e.g. bryozoans, bivalves, and hydroids) that live in the giant kelp canopy

(Clarke 1971, Jones 1971, Quast 1971b, Feder et al. 1974, Bray and Ebeling 1975, Bernstein and Jung 1979, Ebeling et al. 1980, Anderson and Sabado 1995, Hobson and Chess 2001). Among many other carnivorous fishes, kelp bass (*Paralabrax clathratus*), damselfish (*Chromis punctipinnis, Hypsypops rubicundus*), surfperch (embiotocids), lingcod (*Ophiodon elongatus*), cabezon (*Scorpaenichthyes marmoratus*), greenling (*Oxylebius pictus*) and numerous species of rockfish (*Sebastes* spp.) feed on a variety of water column and epibenthic prey (O'Connell 1953, Quast 1971b, Feder et al. 1974, Ellison et al. 1979, Ebeling et al. 1980, Laur and Ebeling 1983, DeMartini and Roberts 1990, Holbrook et al. 1990, Hobson and Chess 2001).

Pinnipeds, birds, and sharks and rays represent the apex predator level in CINP forested areas (Figure 4A). Harbor seals (*Phoca vitulina*) are common in CINP kelp forests where they feed voraciously on fishes (Jones 1981). Various species of seabirds (e.g. brown pelicans, cormorants, gulls, grebes, terns, scoters, etc.) forage on zooplankton, crustaceans and fishes within kelp forests, although it is unknown how much kelp forest productivity fuels bird populations (see review by Foster and Schiel 1985). In addition to the occasional pelagic shark, swell sharks (Cephaloscyllium ventriosum), horn sharks (Heterodontus francisci) and bat rays (Myliobatis californica) have been common kelp forest predators in the past, feeding on crustaceans, fishes, abalones and other molluscs (Feder et al. 1974), but their numbers are decreasing (Dayton et al. 1998). As a final note, southern sea otters (Enhydra lutris), paradigmatic kelp forest apex predators, feed on a diverse array of kelp forest consumers including sea urchins, abalones, other gastropods and many other invertebrates (reviewed in Riedman and Estes 1990, Estes 1996). Sea otters were exterminated off southern California by the fur trade during the 1800s, yet southern expansion of central California populations hint to a possible rebound in southern California sea otter populations. Were sea otters to re-establish

populations in the CINP it is unlikely that their distribution would be impacted by deforestation, as sea otter recovery in central California has generally preceded the disappearance of sea urchin barrens (e.g. Watanabe and Harrold 1991).

Effects of deforestation on food web structure

The main effect of deforestation by sea urchin grazing on the structure of the producer level was to reduce the lush kelp and macroalgal assemblages in forested areas to a few lowlying macroalgae and shut down the production of kelp and macroalgal derived phytodetritus (Figure 4B). This effectively shifted feeding of many primary consumers from attached and phytodetrital kelp and macroalgae to phytoplankton phytodetritus. Although little is known about the trophic importance of live or detrital phytoplankton, benthic microalgae, bacteria, or fungi in this system (Foster and Schiel 1985), these producer groups likely represented the primary conduit of fixed carbon to consumers in deforested areas.

Deforestation also had 2 primary effects on the structure of herbivore-producer linkages (Figure 4B): (1) loss of abalones from the system; (2) >40% reduction in the diversity of sessile invertebrates. Less than 25% of secondary consumer taxa and none of the consumer groups were lost due to deforestation (Figure 4B). Still, the structure of trophic interactions at the secondary consumer level differed strikingly between forested and deforested habitats. Most conspicuous was the almost complete loss of the canopy fish assemblage due to the disappearance of their primary habitat *Macrocystis pyrifera*. Not only are these water column-fishes generalist predators, but also their disappearance often precedes the onset of episodic amphipod grazing outbreaks that can cause local giant kelp deforestation (Tegner and Dayton 1987, Graham 2002). In addition, two forest-associated generalist taxa (*Semicossyphus pulcher* and *Pycnopodia*

helianthoides) represent some of the largest predators in southern California kelp forests and have broad diets that at times can be comprised largely of sea urchins (Cowen 1983, 1986, Foster and Schiel 1985). Whether either of these species help to regulate sea urchin populations (as suggested by Tegner and Dayton 1981) and hamper deforestation at ecologically relevant spatial and temporal scales remains untested. Despite their considerable consumption of nearshore fishes, harbor seals were the only tertiary consumers lost from the deforested food web (Figure 4B), suggesting little impact of deforestation on this consumer level.

Conclusions

The CINP giant kelp forest food web is highly diverse at every trophic level and includes many ubiquitous, generalist consumers. However, that 36% of kelp forest species were identified as forest-associates (25% of which were forest-obligates) and > 90% of all species in the CINP surveys were more common in forested versus deforested area, supports the putatively strong association between the giant kelp *Macrocystis pyrifera* and the kelp forest community. Still, simple comparisons of community profiles between forested and deforested habitats are not ideal for testing the paradigm that *M. pyrifera* is the essential component of this diverse and productive system. First, they do not allow for isolation of the role of *M. pyrifera* energy and habitat provision relative to that of other kelp or non-kelp macroalgal species. Clearly, spatiotemporal variability in *M. pyrifera* productivity and abundance will impact (1) the availability of large pieces of kelp drift (Harrold and Reed 1985) and (2) the presence of kelp surface canopies, both of which will subsequently impact kelp forest species that rely on these resources (e.g. Leighton 1971, Quast 1971b, Ebeling et al. 1980, Coyer 1987, Ambrose and Swarbrick 1987). It is unknown, however, the extent to which the provision of energy and

habitat by other kelp and non-kelp macroalgae may compensate for a localized loss of giant kelp. Many of the forest-associated macroalgae are key habitat-formers providing forage and nursery habitats for invertebrates and fishes. Given the generally low contribution of non-kelp macroalgae to the detrital pool (Zobell 1971, Harrold and Reed 1985), however, it is unlikely that the ubiquitous macroalgae remaining in deforested regions produce much phytodetritus in the CINP. In fact, Harrold and Reed (1985) found that drift algae in a deforested area off San Nicholas Island (south of the CINP) was generally sparser than in a nearby forested area. Second, sea urchin overgrazing causes physical disturbance to the sea floor beyond simply deforestation, again likely impacting the distribution of many sessile invertebrates that attached directly to rocky substrates. Finally, the localized and ephemeral nature of deforested areas in the CINP, although relevant to estimating diversity changes due to deforestation at the monitoring sites, is less useful for understanding the impacts of broader scale kelp deforestation.

The high number of ubiquitous taxa is likely to be in part a real phenomenon and in part an artifact of the generally short duration and localized nature of sea urchin barrens in the CINP. The commonness of generalist consumers and high diversity of trophic linkages for most taxonomic groups (i.e. the lack of reliance on a single food source) is a real characteristic of southern California giant kelp forests. At the same time, the generally high mobility of giant kelp forest consumers and the ephemeral nature of sea urchin barrens in the CINP may have limited the number of forest-associates that were identified herein. Many fishes and invertebrates can move freely among forested and deforested habitats, and many forestassociated but long-lived individuals may simply have outlasted the barrens state. Although individual monitoring sites were widely separated from each other (Figure 1), in some cases a site's transect cut through both types of habitats or included one habitat but ended near the boundary of the other, likely exacerbating this problem. In general, comparison of the food webs for forested and deforested habitats indicated an apparent shift in energy provision from phytodetritus and attached perennial macroalgae to ephemeral micro- and macroalgae and phytoplankton (and likely also dissolved organic carbon and nitrogen; Gerard 1976). The striking loss of the phytodetritus pathway leaves many consumer species with a much more limited selection of available prey. Furthermore, although most consumer groups were represented in deforested habitats, some groups lost individual species that solely accounted for specific predator-prey linkages. Given these conspicuous changes in the apparent food web structure of deforested habitats, many of the CINP 'ubiquitous' species may drop out of the system given loss of available prey due to more prolonged kelp disappearance. As such, the 36% of kelp forest species identified as forest-associates should be considered a conservative estimate.

It is also important to note that most of the data that led to the construction of the forested and deforested food webs came from simple diet studies of kelp forest consumers. In most cases, researchers merely described the variety of prey species eaten, occasionally adding additional information regarding relative importance of individual prey items to the diet (generally based on percent frequency or volume in gut contents). Experimental data on the effect of predators on prey exist only for certain conspicuous predator-prey interactions (e.g. Bernstein and Jung 1979, Schmitt 1982, Cowen 1983, Watanabe 1984b, Anderson 2001). Furthermore, large-scale deforestation of mainland giant kelp forests off Point Loma and Palos Verdes during the 1950's and 60's clearly identified sea urchin grazing as an important trophic linkage in southern California giant kelp forests (North and Hubbs 1968, North and Pearse 1970, North 1971). Episodic mass mortalities of giant kelp due to grazing by amphipods, gastropods and holdfastboring isopods also helped to identify these taxa as having potentially strong roles in this system (North 1971, Leighton 1971, Tegner and Dayton 1987, Graham 2002). Yet, few studies have actually attempted to quantify energy flow or the strength of any given interaction relative to any other. Recently, Sala and Graham (2002) used laboratory feeding trials and field surveys to determine the relative impact of 45 species of kelp forest herbivores (sea urchins, amphipods, isopods, gastropods) on the survival of giant kelp microscopic stages. In the end, they failed to identify any single species as 'keystone' (*sensu* Paine 1969), finding instead that many different species had the potential to have strong impacts on giant kelp recruitment. Still, it is unclear whether such strong impacts reflect important trophic interactions.

With the addition of species abundance and biomass data, the forested-deforested comparisons will facilitate the quantification of more tangible impacts of kelp loss from the system. It is currently impossible to quantify with any degree of certainty the potentially large decreases in secondary productivity that likely accompanied localized deforestation. Such studies will require (1) long-term abundance and biomass data for multiple southern California giant kelp forests, (2) an understanding of the rate of energy flow through the numerous trophic conduits, and (3) long-term manipulations of kelp biomass over broad spatial scales. At present, few tools are available for tracking energy flow through complex food webs. The application of carbon and nitrogen stable isotopes to studying trophic interactions in algal-based marine ecosystems has been limited to just a few systems (Arctic - Dunton and Schell 1987; Aleutian islands - Duggins et al. 1989; Gulf of Alaska - Hobson et al. 1994; Southern Ocean - Kachler et al. 2000; Mediterranean - Pinnegar and Polunin 2000), all of which had far less species diversity than CINP kelp forests. Still, such techniques in conjunction with long-term biomass and abundance data and numerical food web modeling (e.g. ECOPATH) may be useful in examining

the relative importance of habitat provision, energy flow and species interactions in regulating the productivity of this system. Ultimately, a better understanding of the role of deforestation in driving changes kelp forest diversity and productivity will require field manipulations of the abundance of various energy and habitat producing taxa.

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Literature cited

- Ambrose RF. 1984. Food preferences, prey availability and the diet of Octopus bimaculatus. Journal of Experimental Marine Biology & Ecology 77: 29-44.
- Ambrose RF, Swarbrick SL. 1989. Comparison of fish assemblages on artificial and natural reefs off the coast of southern California. Bulletin of Marine Science 44:718-733.
- Anderson TW. 1994. Role of macroalgal structure in the distribution and abundance of a temperate reef fish. Marine Ecology-Progress Series 113:279-290.

- Anderson TW. 2001. Predator responses, prey refuges, and density-dependent mortality of a marine fish. Ecology 82: 245-257.
- Anderson TW, Sabado BD. 1995. Correspondence between food availability and growth of a planktivorous temperate reef fish. Journal of Experimental Marine Biology & Ecology 189:65-76.
- Angel A, Ojeda FP. 2001. Structure and trophic organization of subtidal fish assemblages on the northern Chilean coast: the effect of habitat complexity. Marine Ecology Progress Series 217:81-91.
- Barnes RSK, Hughes RN. 1988. An Introduction to Marine Ecology. Blackwell Science: Oxford.
- Behrens MD, Lafferty KD. Fisher's linear discriminant analysis utilized to describe the kelp forest-urchin barrens dichotomy. Unpublished manuscript.
- Bernstein BB, Jung N. 1979. Selective pressures and co-evolution in a kelp canopy community in southern California, USA. Ecological Monographs 49:335-355.
- Bray, RN, Ebeling AW. 1975. Food activity and habitat of 3 picker-type micro-carnivorous fishes in the kelp forests off Santa Barbara, California, USA. Fishery Bulletin 73:815-829.
- Carr MH. 1989. Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. Journal of Experimental Marine Biology and Ecology 126:59-76.
- Castilla JC. 1985. Food webs and functional aspects of the kelp, *Macrocystis pyrifera*, community in the Beagle Channel, Chile. Siegfried WR, Condy PR, Laws RM, editors.
 Antarctic nutrient cycles and food webs. Germany: Springer-Verlag. p. 407-414.

Clarke WD. 1971. Mysids of the southern kelp region. Nova Hedwigia 32:369-380.

- Cowen, RK. 1983. The effect of sheephead, *Semicossyphus pulcher*, predation on red sea-urchin, *Strongylocentrotus franciscanus*, populations: an experimental analysis. Oecologia 58:249-255.
- Cowen, RK. 1986. Site-specific differences in the feeding ecology of the California sheephead, *Semicossyphus pulcher* (Labridae). Environmental Biology of Fishes 16:193-203.
- Coyer JA. 1985. The invertebrate assemblage associated with the giant kelp *Macrocystis pyrifera* at Santa Catalina Island, California, USA: a general description with emphasis on amphipods, copepods, mysids and shrimps. Fishery Bulletin 82:55-66.
- Coyer JA. 1987. The mollusk assemblage associated with the fronds of giant kelp *Macrocystis pyrifera* at Santa Catalina Island, California, USA. Bulletin Southern California Academy of Sciences 85:129-138.
- Davis GE, Richards DV, Kushner DJ. 1996. Kelp Forest Monitoring Design Review. Technical Report CHIS-96-01. California: Channel Islands National Park, Ventura.
- Dayton PK. 1985. Ecology of kelp communities. Annual Review of Ecology and Systematics 16:215-245.
- Dayton PK, Tegner MJ, Parnell PE, Edwards PB. 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. Ecological Monographs 62:421-445.
- Dayton PK, Tegner MJ, Edwards PB, Riser KL. 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. Ecological Applications 8:309-322.
- Dayton PK, Tegner MJ, Edwards PB, Riser KL. 1999. Temporal and spatial scales of kelp demography: the role of oceanographic climate. Ecological Monographs 69:219-250.
- DeMartini EE, Roberts DA. 1990. Effects of giant kelp (*Macrocystis*) on the density and abundance of fishes in a cobble-bottom kelp forest. Bulletin of Marine Science 46:287-300.

- Duggins DO, Simenstad CA, Estes JA. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. Science 245:170-173.
- Dunton KH, Schell DM. 1987. Dependence of consumers on macroalgal (*Laminaria solidungula*) carbon in an arctic kelp community: δ¹³C evidence. Marine Biology 93:615-625.
- Ebeling AW, Larson RJ, Alevizon BS. 1980. Habitat groups and island-mainland distribution of kelp-bed fishes off Santa Barbara, California. Power DM, editor. The California islands: proceedings of a multidisciplinary symposium. USA: Santa Barbara Museum of Natural History. p. 403-431.
- Edwards MS. 2001. Scale-dependent patterns of community regulation in giant kelp forests. Dissertation. University of California Santa Cruz, USA.
- Ellison JP, Terry C, Stephens JS. 1979. Food resource utilization among five species of embiotocids at King Harbor, California, with preliminary estimates of caloric intake. Marine Biology 52:161-169.
- Estes JA. 1996. The influence of large, mobile predators in aquatic food webs: Examples from sea otters and kelp forests. Greenstreet SPR, Tasker ML, editors. Aquatic predators and their prey. United Kingdom: Blackwell Science Publishers. p. 65-72.
- Feder HM, Turner CH, Limbaugh C. 1974. Observations on fishes associated with kelp beds in southern California. USA: State of California Resources Agency and Fish and Game, Sacramento.
- Foster MS, de Vogelaere AP, Oliver JS, Pearse JS, Harrold C. 1991. Open coast intertidal and shallow subtidal ecosystems of the northeast Pacific. Mathieson AC, Nienhuis PH, editors. Ecosystems of the world: intertidal and littoral ecosystems. Netherlands: Elsevier,

Amsterdam. p. 235-272.

- Foster MS, Schiel DR. 1985. The ecology of giant kelp forests in California: a community profile. US Fish & Wildlife Service Biological Report 85:1-152.
- Foster MS, Schiel DR. 1988. Kelp communities and sea otters: keystone species or just another brick in the wall? VanBlaricom GR, Estes JA, editors. The Community Ecology of Sea Otters. Springer-Verlag: Berlin. p. 92-115.
- Gerard VA. 1976. Some aspects of material dynamics and energy flow in a kelp forest in Monterey Bay, California. Dissertation, University of California Santa Cruz, California, USA, p. 173.
- Graham MH, Harrold C, Lisin S, Light K, Watanabe JM, Foster MS. 1997. Population dynamics of giant kelp *Macrocystis pyrifera* along a wave exposure gradient. Marine Ecology Progress Series 148:269-279.
- Graham MH. 2002. Prolonged reproductive consequences of short-term biomass loss in seaweeds. Marine Biology 140:901-911.
- Graham MH, Dayton PK, Erlandson JM. 2003. Ice ages and ecological transition on temperate coasts. Trends in Ecology and Evolution 18:33-40.
- Harrold C, Pearse JS. 1987. The ecological role of echinoderms in kelp forests. Echinoderm Studies 2:137-233.
- Harrold C, Reed DC. 1985. Food availability, sea urchin grazing, and kelp forest community structure. Ecology 66:1160-1169.
- Hobson KA, Piatt JF, Pitocchelli J. 1994. Using stable isotopes to determine seabird trophic relationships. Journal of Animal Ecology 63:786-798

- Hobson ES, Chess JR. 2001. Influence of trophic relations on form and behavior among fishes and benthic invertebrates in some California marine communities. Environmental Biology of Fishes 60:411-457.
- Holbrook SJ, Carr MH, Schmitt RJ, Coyer JA. 1990. Effect of giant kelp on local abundance of reef fishes: the importance of ontogenetic resource requirements. Bulletin of Marine Science 47:104-114.
- Jackson GA. 1977. Nutrients and production of giant kelp, *Macrocystis pyrifera*, off southern California. Limnology and Oceanography 22:979-995.
- Jackson GA. 1987. Modeling the growth and harvest yield of the giant kelp *Macrocystis pyrifera*. Marine Biology 95:611-624.
- Jones LG. 1971. Studies on selected small herbivorous invertebrates inhabiting *Macrocystis* canopies and holdfasts in southern California kelp beds. Nova Hedwigia 32:343-367.
- Jones RE. 1981. Food habits of smaller marine mammals from northern California. Proceedings of the California Academy of Sciences 44:409-433.
- Kaehler S, Pakhmov EA, McQuaid CD. 2000. Trophic structure of the marine food web at the Prince Edward Islands (Southern Ocean) determined by ∂¹³C and ∂¹⁵N analysis. Marine Ecology Progress Series 208:13-20.
- Laur DR, Ebeling AW. 1983. Predator-prey relationships in surf-perches. Environmental Biology of Fishes 8:217-229.
- Lawrence JM. 1975. On the relationships between marine plants and sea urchins. Oceanography and Marine Biology Annual Review 13:213-286.

- Leet WS, Dewees CM, Klingbeil R, Johnson EJ, editors. 2001. California's living marine resources: a status report. State of California Resources Agency and Fish and Game: Sacramento.
- Leighton DL. 1971. Grazing activities of benthic invertebrates in southern California kelp beds. Nova Hedwigia 32:421-453.
- Mann KH. 1973. Seaweeds: their productivity and strategy for growth. Science 182:975-981.
- Mitchell CT, Turner CH, Strachan AR. 1969. Observations on the biology and behavior of the California spiny lobster, *Panulirus interruptus* (Randall). California Fish and Game 55:121-131.
- Morris RH, Abbott DP, Haderlie EC. 1980. Intertidal Invertebrates of California. Stanford: Stanford University Press.
- North WJ. 1971. The biology of giant kelp beds (*Macrocystis*) in California: Introduction and background. Nova Hedwigia 32:1-68.
- North WJ. 1994. Review of *Macrocystis* biology. Akatsuka I, editor. Biology of Economic Algae. Netherlands: Academic Publishing. p. 447-527.
- North WJ, Hubbs CL, editors. 1968. Utilization of kelp-bed resources in southern California. USA: State of California Resources Agency and Fish and Game, Sacramento.
- North WJ, Pearse JS. 1970. Sea urchin population explosion in southern California coastal waters. Science 167:209.
- O'Connell CP. 1953. The life-history of the cabezon. California Fish & Game 93:1-76
- Paine RT. 1969. A note on trophic complexity and community stability. American Naturalist 103:91-93.
- Parker BC. 1963. Translocation in the giant kelp *Macrocystis*. Science 140:891-892.

Pinnegar JK, Polunin NVC. 2000. Contributions of stable-isotope data to elucidating food webs of Mediterranean rocky littoral fishes. Oecologia 122:399-406.

Quast JC. 1971a. Fish fauna of the rocky inshore zone. Nova Hedwigia 32:481-507.

- Quast JC. 1971b. Observations on the food of the kelp bed fishes. Nova Hedwigia 32:541-579.
- Riedman ML, Estes JA. 1990. The sea otter *Enhydra lutris*: behavior, ecology and natural history. US Fish & Wildlife Service Biological Report 90:1-126.
- Robles C. 1987. Predator foraging characteristics and prey population structure on a sheltered shore. Ecology 68:1502-1514.
- Rosenthal RJ, Clarke WD, Dayton PK. 1974. Ecology and natural history of a stand of giant kelp, *Macrocystis pyrifera*, off Del Mar, California. Fishery Bulletin 72:670-684.
- Sala E, Graham MH. 2002. Community-wide distribution of predator-prey interaction strength in kelp forests. Proceedings of the National Academy of Sciences USA 99:3678-3683
- Schmitt RL. 1982. Consequences of dissimilar defenses against predation in a subtidal marine community. Ecology 63:1588-1601.
- Stebbins, TD. 1986. Density distribution and feeding of the marine snail Norrisia norrisi
 (Mollusca, Gastropoda) on the kelp Macrocystis pyrifera (Phaeophyta, Laminariales).
 Bulletin of the southern California Academy of Sciences 85:69-73.
- Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. Environmental Conservation 29:436-459.
- Tegner MJ, Dayton PK. 1981. Population structure, recruitment and mortality of two sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in a kelp forest. Marine Ecology Progress Series 5:255-268.

- Tegner MJ, Dayton PK. 1987. El Niño effects on southern California kelp forest communities. Advances in Ecological Research 17:243-279.
- Tegner MJ, Levin LA. 1983. Spiny lobsters and sea urchins: analysis of a predator-prey interaction. Journal of Experimental Marine Biology and Ecology 73:125-150.
- Towle DW, Pearse JS. 1973. Production of the giant kelp, *Macrocystis*, estimated by in situ incorporation of ¹⁴C in polyethylene bags. Limnology and Oceanography 18:155-159.
- Wakefield RL, Murray SN. 1998. Factors influencing food choice by the seaweed-eating marine snail *Norrisia norrisi* (Trochidae). Marine Biology 130:631-642.
- Watanabe JM. 1984a. Food preference, food quality and diets of three herbivorous gastropods (Trochidae: *Tegula*) in a temperate kelp forest habitat. Oecologia 62:47-52.
- Watanabe JM. 1984b. The influence of recruitment, competition, and benthic predation on spatial distributions of three species of kelp forest gastropods (Trochidae: *Tegula*). Ecology 65:920-936.
- Watanabe JM, Harrold C. 1991. Destructive grazing by sea urchins *Strongylocentrotus* spp. in a central California kelp forest: potential roles of recruitment, depth, and predation. Marine Ecology Progress Series 71:125-141.
- Zimmerman RC, Robertson DL. 1985. Effects of El Nino on local hydrography and growth of the giant kelp, *Macrocystis pyrifera*, at Santa Catalina Island, California. Limnology and Oceanography 30:1298-1302.
- Zimmerman RC, Kremer JN. 1986. In situ growth and chemical composition of the giant kelp, *Macrocystis pyrifera*: response to temporal changes in ambient nutrient availability. Marine Ecology Progress Series 27:277-285.

Zobell CE. 1971. Drift seaweeds on San Diego County beaches. Nova Hedwigia 32:269-314.

Figure legends.

- Figure 1. Geographic location of the Channel Islands National Park. Inset: Location of the 16 long-term kelp forest monitoring sites.
- Figure 2. Frequency of occurrence of habitat-associated organisms between forested and deforested regions. A. Barrens-associated taxa: found to occur significantly more often in deforested than forested habitats. B. Forest-obligate taxa: found only in forested habitats. C. Forest-associated taxa: found to occur significantly more often in forested than deforested habitats. Shaded bars: number of occurrences in forested surveys; open bars: number of occurrences in deforested surveys. Taxa ordered in decreasing total frequency of occurrence (i.e., forested + deforested). Consumer groupings for individual taxa are listed in Appendix 1.
- Figure 3. Frequency of occurrence of ubiquitous organisms between forested and deforested regions. Ubiquitous taxa: no significant difference in occurrence between forested and deforested habitats. Format the same as in Figure 2.
- Figure 4. Forested (A) and deforested (B) food webs for the Channel Islands National Park.
 Boxes: consumers; Circles: producers; Arrows: energy flow from producers to consumers;
 Dashed lines: phytodetrital pathways. Numbers in parentheses represent the number of 275
 common kelp forest taxa within each taxonomic group (species from Figures 2 & 3,
 Appendix 1). A. Forest-associates and ubiquitous taxa included. B. Barrens-associates and
 ubiquitous taxa included. Species lists were not available for crustose corallines,
 phytoplankton, zooplankton, amphipods & isopods (except *Idotea resecata*), and birds.



Graham Figure 1







Graham Figure 4A



Graham Figure 4B

Appendix 1. Common taxa observed in >12 of 119 (10%) Channel Island National Park (CINP) monitoring surveys (1982-2000). A. Forest associated taxa: found to occur significantly more often in forested than deforested habitats; * indicate forest-obligate taxa. B. Ubiquitous taxa: no significant difference in occurrence between forested and deforested habitats. Lytechinus anamesus (not listed) was the only barrens associated taxon.

A.

PRODUCERS kelp

Dictyoneuropsis reticulata* Eisenia arborea Laminaria farlowii*

Acrosorium venulosum* Bossiella orbigniana Botryocladia pseudodichotoma* *Calliarthron* sp. Callophyllis flabellulata* Callophyllis violacea* *Carpopeltis bushiae* Chondracanthus corymbifera *Codium setchellii* Corallina officinalis Cryptopleura violacea* Cvstoseira osmundacea* Derbesia marina

Macrocystis pyrifera* Pterygophora californica*

other macroalgae

Desmarestia ligulata Dictyopteris undulata Dictyota flabellulata* Fauchea laciniata *Gelidium robustum* Nienburgia andersoniana* Phycodrys setchellii* Plocamium cartilagineum* Rhodoptilum plumosum* Rhodymenia californica Rhodymenia pacifica Zonaria farlowii*

PRIMARY CONSUMERS abalones Haliotis rufescens herbivorous molluscs

Zaolutus actius

isopods

sessile invertebrates anemones Tealia lofotensis

Epiactis prolifera Halcampa decemtentaculata

Haliotis corrugata

Norrisia norrisi

Idotea resecata

Megabalanus californicus

bryozoans

barnacles

Costazia robertsoniae Crisia sp. Diaperoecia californica Eurystomella bilabiata Hippodiplosia insculpta

Abietinaria sp. Aglaophenia latirostris Obelia sp.

Diopatra ornata Phragmatopoma californica

Acarnus erithacus Cliona celata Hymenamphiastra cyanocrypta Leucilla nuttingi Leucosolenia eleanor Ophalitaspongia pennata

Boltenia villosa Clavelina huntsmani

Atherinops affinis Brachyistius frenatus Cymatogaster aggregata* Embiotoca jacksoni Embiotoca lateralis

Doriopsilla albopunctata Fusinus kobelti Homalopoma luridum Maxwellia santarosana

Cancer antennarius Cryptolithodes sitchensis*

Dermasterias imbricata Henricia leviuscula Membranipora membranacea Parasmittina californica* Phidolopora labiata Thalamoporella californica

hydroids

Plumularia sp. Sertularella sp.* Sertularia sp.*

polychaetes

Pista elongata

sponges

Penares cortius* Polymastia pachymastia* Spheciospongia confoederata* Verongia aurea Xestospongia trindinaea

tunicates

Pycnoclavella stanleyi Styela montereyensis

SECONDARY CONSUMERS

carnivorous fishes

Gibbonsia elegans Heterostichus rostratus Hypsurus caryi Sebastes atrovirens Semicossyphus pulcher carnivorous molluscs

> Phidiana hiltoni Pseudomelatoma torosa Triopha catalinae

Lobsters, crabs and shrimps

Hapalogaster cavicauda Pugettia producta*

sea stars

Mediaster aequalis Pycnopodia helianthoides

TERTIARY CONSUMERS pinnipeds

Phoca vitulina

PRODUCERS other macroalgae

Cladophora graminea Codium cuneatum Codium fragile Codium hubbsii Colpomenia peregrina Dictyota binghamiae Fryeella gardneri Gelidium purpurascens Laurencia pacifica Prionitis lanceolata Sciadophycus stellatus Scinaia articulata Ulva lactuca

PRIMARY CONSUMERS brittle stars

Ophiactis simplex Ophioderma panamense Ophioplocus esmarki

Girella nigricans

Acmaea mitra Aplysia californica Diodora arnoldi Lithopoma gibberosum Lithopoma undosum

Cucumaria miniata Cucumaria piperata Cucumaria salma

Centrostephanus coronatus Strongylocentrotus franciscanus

Anthopleura artemisia Anthopleura elegantissima Astrangia lajollensis Balanophyllia elegans Coenocyathus bowersi Corynactis californica

Balanus sp.

Aetea sp. Antropora tincta Ulva lactuca

stars Ophiopteris papillosa

Ophiothrix spiculata

herbivorous fishes

Medialuna californiensis

herbivorous molluscs

Megathura crenulata Tegula aureotincta Tegula eiseni Tegula regina Tonicella lineata

sea cucumbers

Eupentacta quinquesemita Parastichopus parvimensis

sea urchins

Strongylocentrotus purpuratus

sessile invertebrates

anemones

Lophogorgia chilensis Muricea californica Pachycerianthus fimbriatus Paracyathus stearnsi Phyllactis bradleyi Tealia coriacea

barnacles

Conopea galeata

bryozoans

Bugula californica Bugula neritina Heteropora magna Lichenopora novae-zelandiae

Clavularia sp. *Hydractinia milleri*

Chaceia ovoidea Chama arcane Crassedoma giganteum Lima hemphilli

Phoronis vancouverensis

Arctonoe pulchra Chaetopterus variopedatus Dodecaceria fewkesi Eudistylia polymorpha Myxicola infundibulum

Haliclona permollis Leucetta losangelensis

Aplidium californicum Cnemidocarpa finmarkiensis Cystodytes lobatus Didemnum carnulentum Phidolopora pacifica

hydroids

Tubularia sp.

molluscs

Pododesmus cepio Serpulorbis squamigerus Ventricolaria fordii

phoronids

polychaetes

Ophiodromus pugettensis Salmacina tribranchiata Serpula vermicularis Spirobranchus spinosus

sponges

Lissodendoryx topsenti Tethya aurantia

tunicates

Euherdmania claviformis Metandrocarpa taylori Pyura haustor

SECONDARY CONSUMERS

carnivorous fishes

Alloclinus holderi Artedius corallinus Artedius creaseri Aulorhynchus flavidus *Caulolatilus princeps* Chromis punctipinnis Coryphopterus nicholsi Damalichthyes vacca Gobiesox maeandricus *Gymnothorax mordax* Halichoeres semicinctus Hypsypops rubicundus Leiocottus hirundo Lythrypnus dalli Lythrypnus zebra Neoclinus stephansae **Ophiodon elongatus**

Orthonopias triacis Oxyjulis californica Oxylebius pictus Paralabrax clathratus Pleuronichthys coenosus Rathbunella hypoplecta Rhacochilus toxotes Scorpaena guttata Scorpaenichthys marmoratus Sebastes carnatus Sebastes caurinus Sebastes chrysomelas Sebastes mystinus Sebastes serranoides Sebastes serriceps Trachurus symmetricus

carnivorous molluscs

Amphissa versicolor Anisodoris nobilis Berthellina engeli Cadlina luteomarginata Calliostoma annulatum *Calliostoma supragranosum* Ceratostoma foliatum *Ceratostoma nuttalli* Conus californicus Coryphella iodinea Cypraea spadicea Diaulula sandiegensis Flabellinopsis iodinea

Alpheus clamator Betaeus magniteae Herbstia parvifrons Heptacarpus pictus Loxorhynchus crispatus Loxorhynchus grandis Lysmata californica Paguristes sp.

Octopus bimaculatus

Asterina miniata Astropecten armatus Linckia columbiae

Kelletia kelletii Laila cockerelli Maxwellia gemma Mexichromis porterae Mitra idae Navanax inermis Polycera atra Simnia vidleri Trivia californiana Trivia solandri Volvarina taeniolata Lobsters, crabs and shrimps Pagurus sp. Pandalus danae Panulirus interruptus Paraxanthias taylori Pelia tumida Petrolisthes cabrilloi Pugettia richii Scyra acutifrons

Fusinus luteopictus

Hermissenda crassicornis

octopuses

Octopus rubescens

sea stars

Orthasterias koehleri *Pisaster brevispinus* Pisaster giganteus

TERTIARY CONSUMERS

sharks and rays

Cephaloscyllium ventriosum Heterodontus francisci

Myliobatis californica

33