

Effects of Local Deforestation on the Diversity and Structure of Southern California Giant Kelp Forest Food Webs

Michael H. Graham^{1,2}

¹Center for Population Biology, University of California, Davis, California 95616, USA; ²Current address: Moss Landing Marine Labs, B272 Moss Landing Road, Moss Landing, California 95039, USA

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 article, I use a 19-year-long kelp forest-monitoring data set from the Channel Islands National Park (a) to identify associations between subtidal species and forested or deforested habitats, (b) to 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 (c) to 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 (that is, sea urchin barrens); 25 species were found exclusively in forested areas. Most of these

associations were 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 microalgae, macroalgae, and phytoplankton. These results support the reliance of giant kelp forest food-web structure and diversity on the presence of the forest itself.

Key words: 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 and others 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 nonextractive industries, including fisheries, aquaculture, and tourism (Leet and others 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) and 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 three-dimensional

Received 21 October 2002; accepted 25 April 2003; published online 27 April 2004.

Corresponding author; e-mail: mgraham@mlml.calstate.edu

habitats that it provides (Quast 1971a; Feder and others 1974; Ebeling and others 1980; Coyer 1985, 1987; Ambrose and Swarbrick 1989; Holbrook and others 1990) but also by the considerable amounts of fixed carbon (drift kelp) retained within and exported from coastal giant kelp forests [reviewed by Graham and others (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 [for example, the Chilean invertebrate and fish assemblages studied by Castilla (1985) and Angel and Ojeda (2001), respectively] or even individual reefs [for example, see Rosenthal and others (1974)]. A generalized version of the Rosenthal and others' (1974) giant kelp forest food web was developed by Foster and Schiel (1985), who emphasized the fundamental role of algal production, primarily from *M. 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 *M. 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 [for example, episodic storms, El Niño–Southern Oscillation events, or herbivore overgrazing (Zimmerman and Robertson 1985; Zimmerman and Kremer 1986; Dayton and others 1992, 1999; Graham and others 1997; Edwards 2001; Steneck and others 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), and Steneck and others (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 [for example, see Tegner and Dayton (1981, 1987) and Graham (2002)]. Defor-

estation 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), Foster and Schiel (1985), Harrold and Pearse (1987), and Foster and others (1991)], although there has been little attempt to study species-level trophic interactions beyond simple two-species predator–prey linkages [for example, see Schmitt (1982) and Sala and Graham (2002)]. As such, there are not enough data to study rigorously 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, (a) to identify associations between subtidal species and forested or deforested habitats, (b) to generate an idealized giant kelp forest food web for the region, and (c) to determine changes in the diversity and complexity of this food web due to localized deforestation. This article therefore represents the first quantification of the effects of deforestation on an entire kelp forest community.

THE DATA SET

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 and others 1996). The CINP is approximately 1000 km² and surrounds the five 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

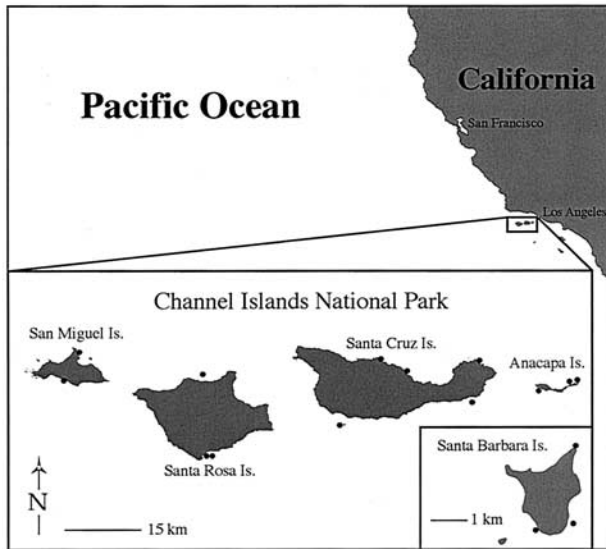


Figure 1 Geographic location of the Channel Islands National Park. Inset: Location of the 16 long-term kelp forest-monitoring sites.

of macroscopic taxa were made twice annually. Surveys were conducted using quadrats, band transects, random point contacts, visual transects, and roving diver counts (Davis and others 1996). Specifically, (a) the distribution of discrete benthic organisms was estimated at each station by using 24 paired 1×1 -m quadrats, 40 continuous and adjacent 1×5 -m quadrats, and 24 paired 3×10 -m band swaths that were systematically arranged along the transect; (b) the distribution of encrusting invertebrates and macroalgae was estimated using 600 nonadjacent points (point contacts) randomly distributed along each transect; and (c) the distribution of fish and pinnipeds was estimated using four $2 \times 3 \times 50$ -m fixed visual transects and a timed roving diver count. A total of 716 taxa were observed during the 19 years of CINF kelp forest monitoring, of which only 275 species were common enough to be observed in more than 12 (10%) of the 119 surveys; 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 and others 1974; Rosenthal and others 1974; Morris and others 1980; Castilla 1985; Dayton 1985; Foster and Schiel 1985; Harold and Pearse 1987; Foster and others 1991; Angel and Ojeda 2001; Hobson and Chess 2001). Based on these studies, taxa from the CINF 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 (for example, sessile invertebrates). These groupings were not based on feeding modes as in the studies by Foster and Schiel (1985), since many of the taxa can effectively utilize more than one mode. Due to broad diets, a few heterotrophic taxa were considered to belong to more than one consumer level (for example, 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 CINF kelp forest-monitoring program has witnessed both short-term 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 (Harold and Pearse 1987). In some cases, multiple transitions between forested and deforested states occurred within a given site. Each of 119 CINF 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); 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 CINF 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 by using a heterogeneity chi-squared (χ^2) analysis: (a) χ^2 statistics comparing forested to deforested habitats were computed for each of the 275 common taxa (using Yates correction for 1 *df* con-

trasts); (b) all 275 statistics were ranked from low to high; (c) a running cumulative heterogeneity χ^2 was estimated; and (d) 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 (that is, species with cumulative $\chi^2 \geq 313.6$) were determined to be *forest associates* or *barrens associates* based on the habitat in which they were most commonly found, and non-significant species were labeled as *ubiquitous*, meaning that 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 and Appendix 1A), whereas 176 species were found to be ubiquitous (Figure 3 and 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 CIMP sites shifted from forested to deforested states was 98 (36%) taxa out of 274. Furthermore, 151 of the 176 ubiquitous species and 251 of the 275 total species observed in the CIMP surveys were more common in forested versus deforested 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 *Cymatogaster aggregata* and the canopy-dwelling kelp crab *Pugettia producta* corresponded with their attraction to *M. pyrifera* canopies, whereas the umbrella crab *Cryptolithoides stichensis* was likely a forest obligate, due to its use of foliose macroalgal and geniculate coralline habitats as cover.

Published natural history studies have described clear functional ties to the presence of macroalgae

(and *M. pyrifera* in particular) for many of the 73 nonobligate 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 (for example, sessile invertebrates) use kelp phytodetritus 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 and others 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 are likely structural. The forest association of sessile invertebrates directly attached to rocks, however, is probably due to direct impacts of sea urchin movements rather than to the actual loss of macroalgae.

Numerous nonsessile 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 *M. pyrifera* [see also Ambrose and Swarbrick (1989) and Holbrook and others (1990)]. For example, most field observations in the CIMP (and elsewhere) of the gastropod *Norrisia norrisi*, the isopod *Idotea resicata*, and the carnivorous fishes *Brachyistius frenatus*, *Sebastes atrovirens*, and *Heterostichus rostratus* occur within and around *M. pyrifera* canopies [for example, see Feder and others (1974), Ebeling and others (1980), Coyer (1985), Stebbins (1986), Anderson (1994), and Hobson and Chess (2001)]; Holbrook and colleagues (1990) similarly observed significant increases in the density of *B. frenatus*, *S. atrovirens*, and *H. rostratus* with increased *M. pyrifera* abundance. Many noncanopy 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 and others 1980) and may have a structural association with *M. pyrifera*. Many of the nonobligate forest associations appeared to be due primarily to the presence of *M. pyrifera* in forested areas.

On the other hand, forest associations of the

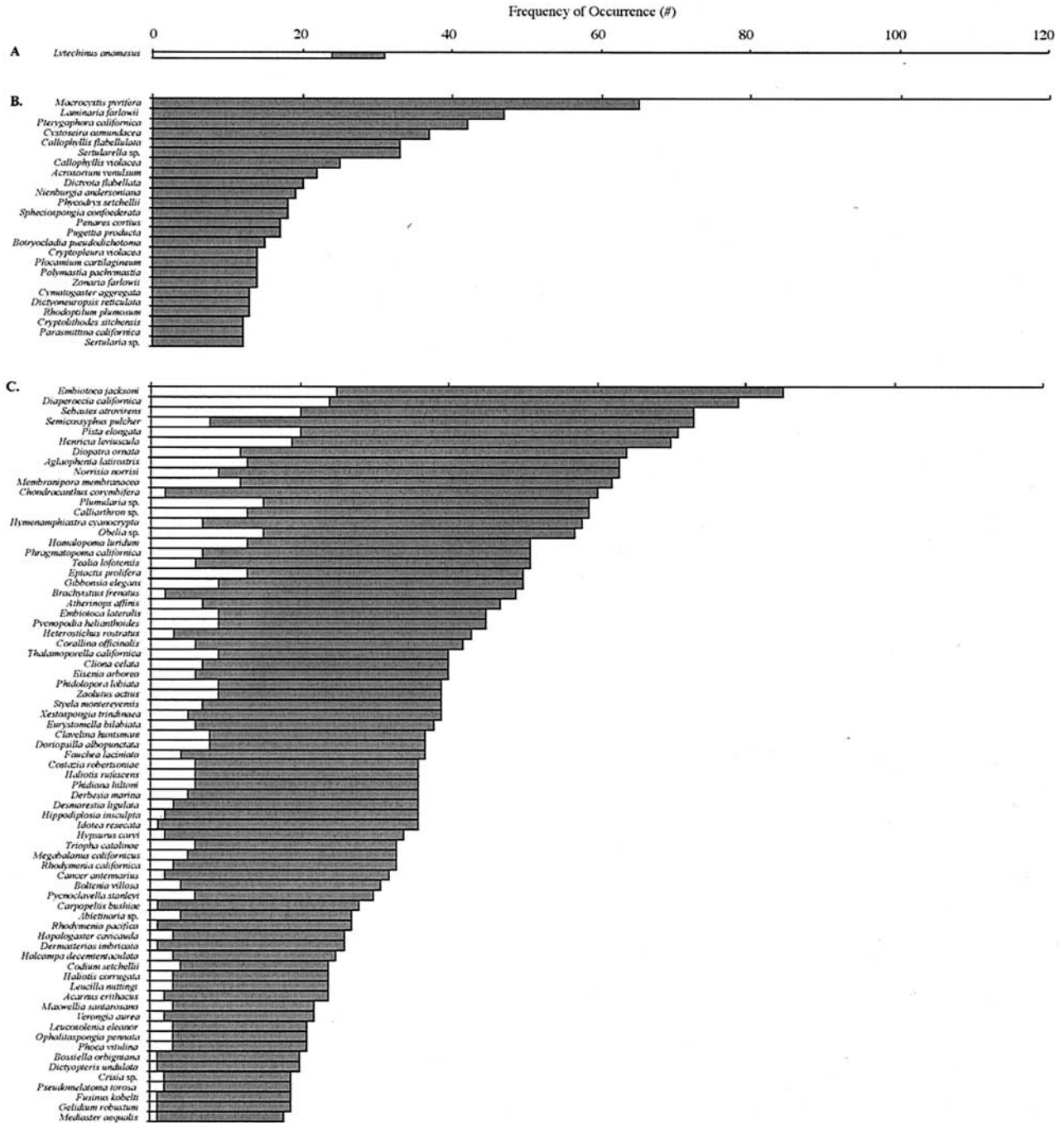
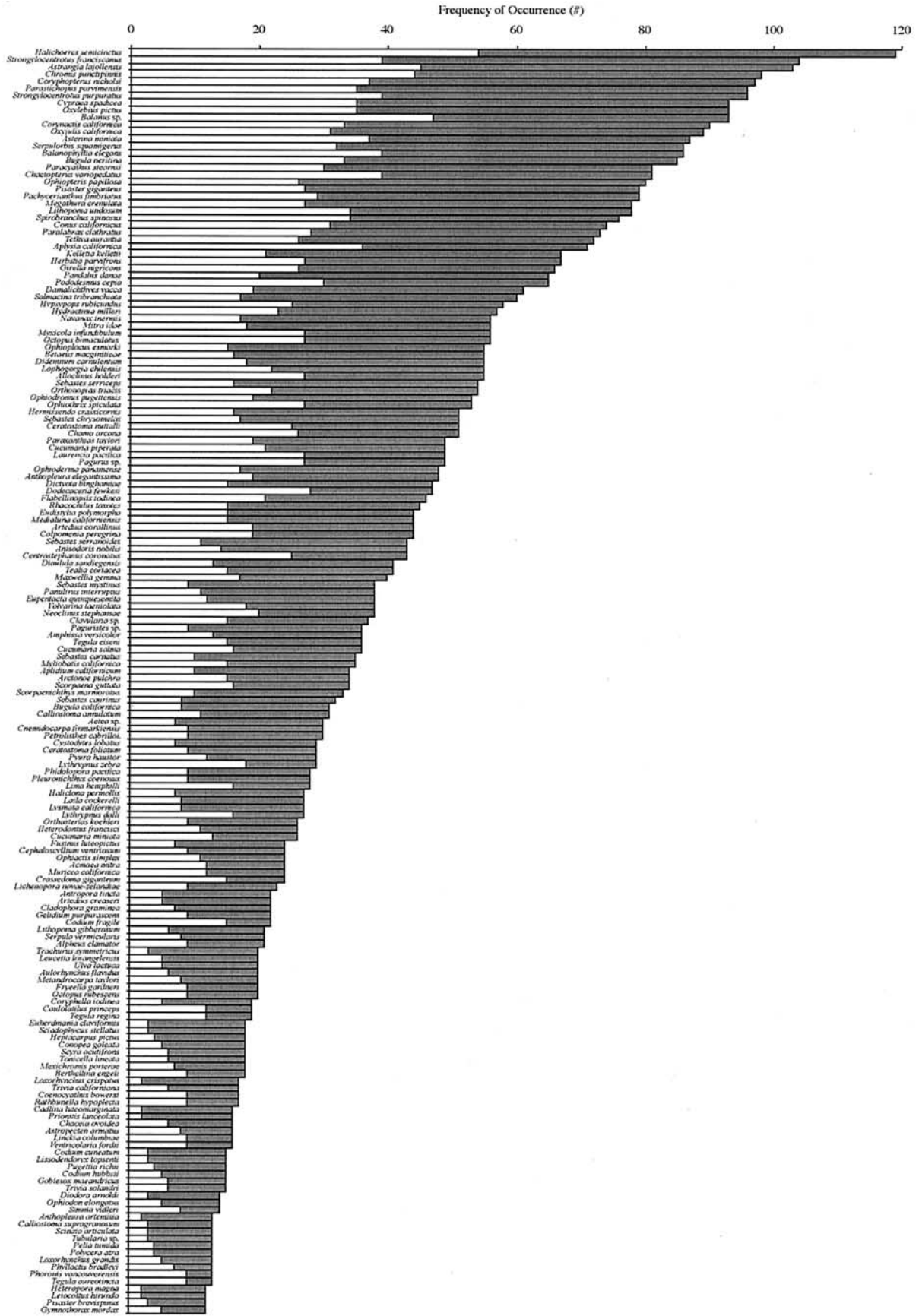


Figure 2 Frequency of occurrence of habitat-associated organisms between forested and deforested regions. A: Barrens-associated taxa: found to occur significantly more often in deforested than in forested habitats. B: Forest-obligate taxa: found only in forested habitats. C: Forest-associated taxa: found to occur significantly more often in forested than deforested habitats. Shaded bars, number of occurrences in forested surveys; and open bars, number of occurrences in deforested surveys. Taxa ordered in decreasing total frequency of occurrence (that is, forested + deforested). Consumer groupings for individual taxa are listed in Appendix 1.

fishes *Embiotoca jacksoni*, *E. lateralis*, and *Gibbonsia elegans* were likely due to habitat modifications other than kelp loss. Specifically, Carr (1989) and Holbrook and colleagues (1990) found that the

abundance of *E. jacksoni* was positively related to *M. pyrifera* abundance due to use 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 nonkelp macroalgae. However, aside from *Laurencia pacifica*, *Dictyota binghamiae*, the opportunist *Colpomenia peregrina*, and *Codium fragile*, no nonkelp 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 were forest associates. That the two herbivorous fishes, *Girella nigricans* and *Medialuna californiensis*, were commonly found in deforested habitats suggested that they could either (a) feed on the remaining macroalgal assemblages, (b) shift diets more toward small invertebrates, or (c) 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 *M. pyrifera* [reviewed by Holbrook and others (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 *M. pyrifera*, has the highest productivity and biomass per square meter [reviewed by Foster and Schiel (1985) and North (1994)]. The other four kelps

represented stipitate subcanopy (*Eisenia arborea* and *Pterygophora californica*) and nonstipitate low-lying forms (*Dictyoneuroopsis reticulata* and *Laminaria farlowii*). A highly diverse nonkelp 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 (nongeniculate) coralline algae (presumably *Lithothamnion/Lithophyllum*). These kelp and nonkelp 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 macroalgal based 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 (for example, *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 and others 1974; Hobson and Chess 2001). Numerous herbivorous mollusks graze directly on kelp stipes, blades, and their associated epibionts [for example, *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 [for example, *Lithopoma* spp. (Leighton 1971)]. Surprisingly, except for *Idotea resicata*, 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).

←
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. The format is the same as in Figure 2.

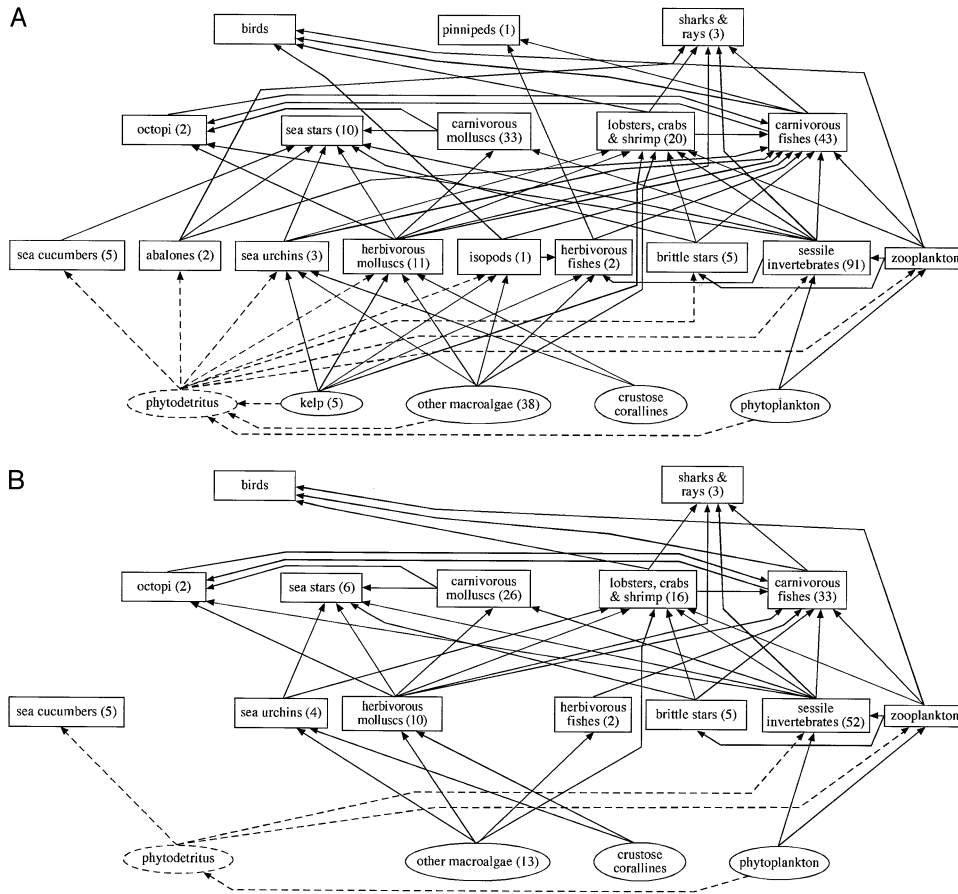


Figure 4 Forested (**A**) and deforested (**B**) food webs for the Channel Islands National Park: *boxes*, consumers; *circles*, producers; *arrows*, energy flow from producers to consumers; and *dashed lines*, phytodetrital pathways. *Numbers in parentheses* represent the number of 275 common kelp forest taxa within each taxonomic group (species from Figures 2 and 3; see 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, and isopods (except *Idotea resicata*), and birds.

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 stronglycentrotid sea urchins (Leighton 1971) and can also be used 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 [for example, 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 molluscs prey upon sessile and slow-moving mobile invertebrates (Mitchell and others 1969; Rosenthal and others 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 [for example, decapods, gastropods, and carnivorous fishes (Rosenthal and others 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 and others 1974; Cowen 1983, 1986; Hobson and Chess 2001). Señorita (*Oxyjulis californica*), kelpfish (*Gibbonsia elegans* and *Heterostichus rostratus*), kelp perch (*Brachyistius frenatus*), and juvenile rockfish (*Sebastes* spp) feed on mysids, amphipods, isopods, and kelp epibionts (for example, bryozoans, bivalves, and hydroids) that live in the giant kelp canopy (Clarke 1971; Jones 1971; Quast 1971b; Feder and others 1974; Bray and Ebeling 1975; Bernstein and Jung 1979; Ebeling and others 1980; Anderson and Sabado 1995; Hobson and Chess 2001). Among many other carnivorous fishes, kelp bass (*Paralabrax clathratus*), damselfish (*Chromis punctipinnis* and *Hypsypops rubicundus*), surfperch (embiotocids), lingcod (*Ophiodon elongatus*), cabezon (*Scorpaenichthys 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 and others 1974; Ellison and others 1979; Ebeling and others 1980; Laur and Ebeling 1983; DeMartini and Roberts 1990; Holbrook and others 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 (brown pelicans, cormorants, gulls, grebes, terns, scoters, and so on) forage on zooplankton, crustaceans, and fishes within kelp forests, although it is unknown how much kelp forest productivity fuels bird populations [see the 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 mollusks (Feder and others 1974), but their numbers are decreasing (Dayton and others 1998).

Dayton and others (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 by Riedman and Estes (1990) and 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 affected by deforestation, as sea otter recovery in Central California has generally preceded the disappearance of sea urchin barrens [for example, see 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 low-lying 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 two primary effects on the structure of herbivore–producer linkages (Figure 4B): (a) loss of abalones from the system and (b) more than 40% reduction in the diversity of sessile invertebrates. Less than 25% of secondary consumer taxa and none of the secondary 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 *M. 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 *Pygocypoda 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 more than 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 nonkelp macroalgal species. Clearly,

spatiotemporal variability in *M. pyrifera* productivity and abundance will affect (a) the availability of large pieces of kelp drift (Harrold and Reed 1985) and (b) the presence of kelp surface canopies, both of which will subsequently affect kelp forest species that rely on these resources [for example, see Leighton (1971), Quast (1971b), Ebeling and others (1980), Coyer (1987), and Ambrose and Swarbrick (1989)]. It is unknown, however, the extent to which the provision of energy and habitat by other kelp and nonkelp 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 nonkelp 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 affecting 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 (that is, 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 forest-associated 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 microalgae 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 [for example, see Bernstein and Jung (1979), Schmitt (1982), Cowen (1983), Watanabe (1984b), and Anderson (2001)]. Furthermore, large-scale deforestation of mainland giant kelp forests off Point Loma and Palos Verdes during the 1950s and 1960s 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 holdfast-boring 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). Few studies, though, 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, and 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 (a) long-term abundance and biomass data for multiple Southern California giant kelp forests, (b) an understanding of the rate of energy flow through the numerous trophic conduits, and (c) 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 and others 1989), Gulf of Alaska (Hobson and others 1994), Southern Ocean (Kaehler and others 2000), and Mediterranean (Pinnegar and Polunin 2000)], all of which had far less species diversity than do CINP kelp forests. Still, such techniques in conjunction with long-term biomass and abundance data and numerical food-web modeling (for example, 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 to kelp forest diversity and productivity will require field manipulations of the abundance of various energy and habitat producing taxa.

ACKNOWLEDGEMENTS

I thank D. Kushner of the CINP kelp forest-monitoring program for providing the CINP species lists, and M. Behrens and K. Lafferty for generously providing me with their unpublished identification of CINP forested and deforested sites. Thanks also to M. Behrens, M. Carr, P. Dayton, M. Edwards, J. Estes, L. Ferry-Graham, M. Foster, R. Grosberg, B. Kinlan, J. Pearse, P. Raimondi, K. Riser, E. Sala, J. Stachowicz, M. Tegner, and numerous others for their discussions of the natural history of giant kelp forest organisms. L. Ferry-Graham, M. Foster, B. Santelices and an anonymous reviewer provided critical reviews of this article. A University of California Faculty Fellowship supported this research.

Appendix 1

Table 1 Common taxa observed in more than 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

Producers

Kelp

*Dictyoneuropsis reticulata**

Eisenia arborea

*Laminaria farlowii**

*Macrocystis pyrifera**

*Pterygophora californica**

Other macroalgae

*Acrosorium venulosum**

Bossiella orbigniana

*Botryocladia pseudodichotoma**

Calliarthron sp.

*Callophyllis flabellulata**

*Callophyllis violacea**

Carpopeltis bushiae

Chondracanthus corymbifera

Codium setchellii

Corallina officinalis

*Cryptopleura violacea**

*Cystoseira osmundacea**

Derbesia marina

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 corrugata

Haliotis rufescens

Herbivorous molluscs

Norrisia norrisi

Isopods

Idotea resicata

Sessile invertebrates

Anemones

Epiactis prolifera

Halcampa decententaculata

Tealia lofotensis

Zaolutus actius

Barnacles

Megabalanus californicus

Bryozoans

Costazia robertsoniae

Crisia sp.

Table 1 (Continued)

Diaperoecia californica
Eurystomella bilabiata
Hippodiplosia insculpta
Membranipora membranacea
*Parasmittina californica**
Phidolopora labiata
Thalamoporella californica

Hydroids
Abietinaria sp.
Aglaophenia latirostris
Obelia sp.
Plumularia sp.
Sertularella sp.*
Sertularia sp.*

Polychaetes
Diopatra ornata
Phragmatopoma californica
Pista elongata

Sponges
Acarnus erithacus
Cliona celata
Hymenamphiastra cyanocrypta
Leucilla nuttingi
Leucosolenia eleanor
Ophalittaspongia pennata
*Penares cortius**
*Polymastia pachymastia**
*Sphaciospongia confederata**
Verongia aurea
Xestospongia trindinaea

Tunicates
Boltenia villosa
Clavelina huntsmani
Pycnoclavella stanleyi
Styela montereyensis

Secondary consumers

Carnivorous fishes
Atherinops affinis
Brachyistius frenatus
*Cymatogaster aggregata**
Embiotoca jacksoni
Embiotoca lateralis
Gibbonsia elegans
Heterostichus rostratus
Hypsurus caryi
Sebastes atrovirens
Semicossyphus pulcher

Carnivorous molluscs
Doriopsilla albopunctata
Fusinus kobelti
Homalopoma luridum
Maxwellia santarosana
Phidiana hiltoni
Pseudomelatoma torosa
Triopha catalinae

Lobsters, crabs and shrimps
Cancer antennarius
*Cryptolithodes sitchensis**

Table 1 (Continued)

Hapalogaster cavicauda
*Pugettia producta**

Sea stars
Dermasterias imbricata
Henricia leviuscula
Mediaster aequalis
Pycnopodia helianthoides

Tertiary consumers

Pinnipeds
Phoca vitulina

B: Ubiquitous taxa: no significant difference between forested and deforested habitats

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
Ophiopteris papillosa
Ophiothrix spiculata

Herbivorous fishes
Girella nigricans
Medialuna californiensis

Herbivorous molluscs
Acmaea mitra
Aplysia californica
Diodora arnoldi
Lithopoma gibberosum
Lithopoma undosum
Megathura crenulata
Tegula aureotincta
Tegula eiseni
Tegula regina
Tonicella lineata

Sea cucumbers
Cucumaria miniata
Cucumaria piperata
Cucumaria salma
Eupentacta quinquesemita
Parastichopus parvimensis

Sea urchins
Centrostephanus coronatus
Strongylocentrotus franciscanus
Strongylocentrotus purpuratus

Table 1 (Continued)

Sessile invertebrates

Anemones

Anthopleura artemisia

Anthopleura elegantissima

Astrangia lajollensis

Balanophyllia elegans

Coenocyathus bowersi

Corynactis californica

Lophogorgia chilensis

Muricea californica

Pachycerianthus fimbriatus

Paracyathus stearnsi

Phyllactis bradleyi

Tealia coriacea

Barnacles

Balanus sp.

Conopea galeata

Bryozoans

Aetea sp.

Antropora tinctoria

Bugula californica

Bugula neritina

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

Fusinus luteopictus

Hermisenda crassicornis

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

Alpheus clamator

Betaeus magniteae

Herbstia parvifrons

Heptacarpus pictus

Loxorhynchus crispatus

Loxorhynchus grandis

Lysmata californica

Paguristes sp.

Table 1 (Continued)

Pagurus sp.

Pandalus danae

Panulirus interruptus

Paraxanthias taylori

Pelia tumida

Petrolisthes cabrilloi

Pugettia richii

Scyra acutifrons

Octopuses

Octopus bimaculatus

Octopus rubescens

Sea stars

Asterina miniata

Astropecten armatus

Linckia columbiae

Orthasterias koehlerii

Pisaster brevispinus

Pisaster giganteus

Tertiary consumers

Sharks and rays

Cephaloscyllium ventriosum

Heterodontus francisci

Myliobatis californica

Abietinaria sp.

Aglaothenia latirostris

Obelia sp.

Plumularia sp.

Sertularella sp.*

Sertularia sp.*

Polychaetes

Diopatra ornata

Phragmatopoma californica

Pista elongata

Sponges

Acarus erithacus

Cliona celata

Hymenamphiastra cyanocrypta

Leucilla nuttingi

Leucosolenia eleanor

Ophalitospongia pennata

*Penares cortius**

*Polymastia pachymastia**

*Sphaciospongia confederata**

Verongia aurea

Xestospongia trindinaea

Tunicates

Boltenia villosa

Clavelina huntsmani

Pycnoclavella stanleyi

Styela montereyensis

Secondary consumers

Carnivorous fishes

Atherinops affinis

Brachyistius frenatus

*Cymatogaster aggregata**

Embiotoca jacksoni

Embiotoca lateralis

Gibbonsia elegans

Table 1 (Continued)

Heterostichus rostratus
Hypsurus caryi
Sebastes atrovirens
Semicossyphus pulcher

Carnivorous molluscs
Doriopsilla albopunctata
Fusinus kobelti
Homalopoma luridum
Maxwellia santarosana
Phidiana hiltoni
Pseudomelatoma torosa
Triopha catalinae

Lobsters, crabs, and shrimps
Cancer antennarius
*Cryptolithodes sitchensis**
Hapalogaster cavicauda
*Pugettia producta**

Sea stars
Dermasterias imbricata
Henricia leviuscula
Mediaster aequalis
Pycnopodia helianthoides

Tertiary consumers

Pinnipeds
Phoca vitulina

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
Fusinus luteopictus
Hermisenda crassicornis
Kelletia kelleitii
Laila cockerelli
Maxwellia gemma
Mexichromis porterae
Mitra idae
Navanax inermis
Polycera atra
Simnia vidleri
Trivia californiana
Trivia solandri
Volvarina taeniolata

Lobsters, crabs, and shrimps
Alpheus clamator
Betaeus magniteae
Herbstia parvifrons
Heptacarpus pictus
Loxorhynchus crispatus

Table 1 (Continued)

Loxorhynchus grandis
Lysmata californica
Paguristes sp.
Pagurus sp.
Pandalus danae
Panulirus interruptus
Paraxanthias taylora
Pelia tumida
Petrolisthes cabrilloi
Pugettia richii
Scyra acutifrons

Octopuses
Octopus bimaculatus
Octopus rubescens

Sea stars
Asterina miniata
Astropecten armatus
Linckia columbiae
Orthasterias koehleri
Pisaster brevispinus
Pisaster giganteus

Tertiary consumers

Sharks and rays
Cephaloscyllium ventriosum
Heterodontus francisci
Myliobatis californica
Heteropora magna
Lichenopora novae-zelandiae
Phidolopora pacifica

Hydroids
Clavularia sp.
Hydractinia milleri
Tubularia sp.

Molluscs
Chacea ovoidea
Chama arcane
Crassedoma giganteum
Lima hemphilli
Pododesmus cepio
Serpulorbis squamigerus
Ventricolaria fordii

Phoronids
Phoronis vancouverensis

Polychaetes
Arctonoe pulchra
Chaetopterus variopedatus
Dodecaceria fewkesi
Eudistylia polymorpha
Myxicola infundibulum
Ophiodromus pugettensis
Salmacina tribranchiata
Serpula vermicularis
Spirobranchus spinosus

Sponges
Haliclona permollis
Leucetta losangelensis
Lissodendoryx topsenti
Tethya aurantia

Table 1 (Continued)

Tunicates

Aplidium californicum
Cnemidocarpa finmarkiensis
Cystodytes lobatus
Didemnum carnulentum
Euherdmania claviformis
Metandrocarpa taylora
Pyura haustor

Secondary consumers

Carnivorous fishes

Alloclinus holderi
Arteidius corallinus
Arteidius 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

*Forest-obligate taxa.

Ubiquitous taxa: no significant difference in occurrence between forested and deforested habitats.

Lytechinus anamesus (not listed) was the only barrens associated taxon.

REFERENCES

- Ambrose RF. 1984. Food preferences, prey availability and the diet of *Octopus bimaculatus*. *J Exp Mar Biol Ecol* 77:29–44.
- Ambrose RF, Swarbrick SL. 1989. Comparison of fish assemblages on artificial and natural reefs off the coast of Southern California. *Bull Mar Sci* 44:718–33.
- Anderson TW. 1994. Role of macroalgal structure in the distribution and abundance of a temperate reef fish. *Mar Ecol Prog Ser* 113:279–90.
- Anderson TW. 2001. Predator responses, prey refuges, and density-dependent mortality of a marine fish. *Ecology* 82:245–57.
- Anderson TW, Sabado BD. 1995. Correspondence between food availability and growth of a planktivorous temperate reef fish. *J Exp Mar Biol Ecol* 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. *Mar Ecol Prog Ser* 217:81–91.
- Barnes RSK, Hughes RN. 1988. An introduction to marine ecology. 2nd ed. Oxford: Blackwell, pp 351 p.
- Bernstein BB, Jung N. 1979. Selective pressures and co-evolution in a kelp canopy community in Southern California, USA. *Ecol Monogr* 49:335–55.
- Bray RN, Ebeling AW. 1975. Food activity and habitat of three "picker-type" micro-carnivorous fishes in the kelp forests off Santa Barbara, California, USA. *Fish Bull* 73:815–29.
- Carr MH. 1989. Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. *J Exp Mar Biol Ecol* 126:59–76.
- Castilla JC. 1985. Food webs and functional aspects of the kelp, *Macrocystis pyrifera*, community in the Beagle Channel, Chile. In: Siegfried WR, Condy PR, Laws RM, Eds. Antarctic nutrient cycles and food webs Germany: Springer-Verlag. p 407–14.
- Clarke WD. 1971. Mysids of the southern kelp region. *Nova Hedwigia* 32:369–80.
- Cowen RK. 1983. The effect of sheephead, *Semicossyphus pulcher*, predation on red sea-urchin, *Strongylocentrotus franciscanus*, populations: an experimental analysis. *Oecologia (Berl)* 58: 249–55.
- Cowen RK. 1986. Site-specific differences in the feeding ecology of the California sheephead, *Semicossyphus pulcher* (Labridae). *Environ Biol 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. *Fish Bull* 82:55–66.
- Coyer JA. 1987. The mollusk assemblage associated with the fronds of giant kelp *Macrocystis pyrifera* at Santa Catalina Island, California, USA. *Bull South Calif Acad Sci* 85:129–38.
- Davis GE, Richards DV, Kushner DJ. 1996. Kelp forest monitoring design review. Technical report CHIS-96-01. Ventura (CA): Channel Islands National Park.
- Dayton PK. 1985. Ecology of kelp communities. *Annu Rev Ecol Syst* 16:215–45.
- Dayton PK, Tegner MJ, Edwards PB, Riser KL. 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecol Appl* 8:309–22.
- Dayton PK, Tegner MJ, Edwards PB, Riser KL. 1999. Temporal and spatial scales of kelp demography: the role of oceanographic climate. *Ecol Monogr* 69:219–50.
- Dayton PK, Tegner MJ, Parnell PE, Edwards PB. 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecol Monogr* 62:421–45.
- DeMartini EE, Roberts DA. 1990. Effects of giant kelp (*Macrocystis*) on the density and abundance of fishes in a cobble-bottom kelp forest. *Bull Mar Sci* 46:287–300.
- Duggins DO, Simenstad CA, Estes JA. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* 245:170–3.

- Dunton KH, Schell DM. 1987. Dependence of consumers on macroalgal (*Laminaria solidungula*) carbon in an arctic kelp community: $\delta^{13}\text{C}$ evidence. *Mar Biol* 93:615–25.
- Ebeling AW, Larson RJ, Alevizon BS. 1980. Habitat groups and island–mainland distribution of kelp-bed fishes off Santa Barbara, California. In: Power DM, Eds. *The California Islands: proceedings of a multidisciplinary symposium Santa Barbara (CA): Santa Barbara Museum of Natural History*. p 403–31.
- Edwards MS. 2001. Scale-dependent patterns of community regulation in giant kelp forests [PhD dissertation]. Santa Cruz: University of California. 140 p.
- 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. *Mar Biol* 52: 161–9.
- Estes JA. 1996. The influence of large, mobile predators in aquatic food webs: examples from sea otters and kelp forests. In: Greenstreet SPR, Tasker ML, Eds. *Aquatic predators and their prey* London: Blackwell. p 65–72.
- Feder HM, Turner CH, Limbaugh C. 1974. Observations on fishes associated with kelp beds in Southern California. *Calif Dep Fish Game Fish Bull* 160:1–144.
- Foster MS, De Vogelaere AP, Oliver JS, Pearse JS, Harrold C. 1991. Open coast intertidal and shallow subtidal ecosystems of the northeast Pacific. In: Mathieson AC, Nienhuis PH, Eds. *Ecosystems of the world: intertidal and littoral ecosystems* Amsterdam: Elsevier. p 235–72.
- Foster MS, Schiel DR. 1985. The ecology of giant kelp forests in California: a community profile. *US Fish Wildl Serv Biol Rep* 85:1–152.
- Foster MS, Schiel DR. 1988. Kelp communities and sea otters: keystone species or just another brick in the wall? In: VanBlaricom GR, Estes JA, Eds. *The community ecology of sea otters* Berlin: Springer-Verlag. p 92–115.
- Gerard VA. 1976. Some aspects of material dynamics and energy flow in a kelp forest in Monterey Bay, California [PhD dissertation]. Santa Cruz: University of California. p 173.
- Graham MH. 2002. Prolonged reproductive consequences of short-term biomass loss in seaweeds. *Mar Biol* 140:901–11.
- Graham MH, Dayton PK, Erlandson JM. 2003. Ice ages and ecological transition on temperate coasts. *Trends Ecol Evol* 18:33–40.
- 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. *Mar Ecol Prog Ser* 148: 269–79.
- Harrold C, Pearse JS. 1987. The ecological role of echinoderms in kelp forests. *Echinoderm Stud* 2:137–233.
- Harrold C, Reed DC. 1985. Food availability, sea urchin grazing, and kelp forest community structure. *Ecology* 66:1160–9.
- Hobson ES, Chess JR. 2001. Influence of trophic relations on form and behavior among fishes and benthic invertebrates in some California marine communities. *Environ Biol Fishes* 60: 411–57.
- Hobson KA, Piatt JF, Pitocchelli J. 1994. Using stable isotopes to determine seabird trophic relationships. *J Anim Ecol* 63:786–98.
- 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. *Bull Mar Sci* 47:104–14.
- Jackson GA. 1977. Nutrients and production of giant kelp, *Macrocystis pyrifera*, off Southern California. *Limnol Oceanogr* 22: 979–95.
- Jackson GA. 1987. Modeling the growth and harvest yield of the giant kelp *Macrocystis pyrifera*. *Mar Biol* 95:611–24.
- Jones LG. 1971. Studies on selected small herbivorous invertebrates inhabiting *Macrocystis* canopies and holdfasts in Southern California kelp beds. *Nova Hedwigia* 32:343–67.
- Jones RE. 1981. Food habits of smaller marine mammals from Northern California. *Proc Calif Acad Sci* 44:409–33.
- Kaehler S, Pakhmov EA, McQuaid CD. 2000. Trophic structure of the marine food web at the Prince Edward Islands (Southern Ocean) determined by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Mar Ecol Prog Ser* 208:13–20.
- Laur DR, Ebeling AW. 1983. Predator–prey relationships in surf-perches. *Environ Biol Fishes* 8:217–29.
- Lawrence JM. 1975. On the relationships between marine plants and sea urchins. *Oceanogr Mar Biol Annu Rev* 13:213–86.
- Leet WS, Dewees CM, Klingbeil R, Johnson EJ, editors. 2001. *California's living marine resources: a status report*. Sacramento: State of California Resources Agency and Fish and Game. 593 p.
- Leighton DL. 1971. Grazing activities of benthic invertebrates in Southern California kelp beds. *Nova Hedwigia* 32:421–53.
- Mann KH. 1973. Seaweeds: their productivity and strategy for growth. *Science* 182:975–81.
- Mitchell CT, Turner CH, Strachan AR. 1969. Observations on the biology and behavior of the California spiny lobster, *Panulirus interruptus* (Randall). *Calif Fish Game* 55:121–31.
- Morris RH, Abbott DP, Haderlie EC. 1980. *Intertidal invertebrates of California*. Stanford: Stanford University Press, pp 104 p.
- 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. In: Akatsuka I, Eds. *Biology of economic algae* The Hague: Academic. p 447–527.
- North WJ, Hubbs CL, editors. 1968. *Utilization of kelp-bed resources in Southern California*. *Calif Dep Fish Game Fish Bull* 139.
- 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. *Calif Fish Game* 93:1–76.
- Paine RT. 1969. A note on trophic complexity and community stability. *Am Nat* 103:91–3.
- Parker BC. 1963. Translocation in the giant kelp *Macrocystis*. *Science* 140:891–2.
- Pinnegar JK, Polunin NVC. 2000. Contributions of stable-isotope data to elucidating food webs of Mediterranean rocky littoral fishes. *Oecologia (Berl)* 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* 32:541–79.
- Riedman ML, Estes JA. 1990. The sea otter *Enhydra lutris*: behavior, ecology and natural history. *US Fish Wildl Serv Biol Rep* 90:1–126.
- Robles C. 1987. Predator foraging characteristics and prey population structure on a sheltered shore. *Ecology* 68:1502–14.
- Rosenthal RJ, Clarke WD, Dayton PK. 1974. Ecology and natural

- history of a stand of giant kelp, *Macrocystis pyrifera*, off Del Mar, California. Fish Bull 72:670–84.
- Sala E, Graham MH. 2002. Community-wide distribution of predator–prey interaction strength in kelp forests. Proc Natl Acad Sci USA 99:3678–83.
- Schmitt RL. 1982. Consequences of dissimilar defenses against predation in a subtidal marine community. Ecology 63:1588–601.
- Stebbins TD. 1986. Density distribution and feeding of the marine snail *Norrisia norrisi* (Mollusca, Gastropoda) on the kelp *Macrocystis pyrifera* (Phaeophyta, Laminariales). Bull South Calif Acad Sci 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. Environ Conserv 29:436–59.
- Tegner MJ, Dayton PK. 1981. Population structure, recruitment and mortality of two sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in a kelp forest. Mar Ecol Prog Ser 5:255–68.
- Tegner MJ, Dayton PK. 1987. El Niño effects on Southern California kelp forest communities. Adv Ecol Res 17:243–79.
- Tegner MJ, Levin LA. 1983. Spiny lobsters and sea urchins: analysis of a predator–prey interaction. J Exp Mar Biol Ecol 73:125–50.
- Towle DW, Pearse JS. 1973. Production of the giant kelp, *Macrocystis*, estimated by in situ incorporation of ^{14}C in polyethylene bags. Limnol Oceanogr 18:155–9.
- Wakefield RL, Murray SN. 1998. Factors influencing food choice by the seaweed-eating marine snail *Norrisia norrisi* (Trochidae). Mar Biol 130:631–42.
- Watanabe JM. 1984a. Food preference, food quality and diets of three herbivorous gastropods (Trochidae: *Tegula*) in a temperate kelp forest habitat. Oecologia (Berl) 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 65:920–36.
- 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. Mar Ecol Prog Ser 71:125–41.
- 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. Mar Ecol Prog Ser 27:277–85.
- Zimmerman RC, Robertson DL. 1985. Effects of El Niño on local hydrography and growth of the giant kelp, *Macrocystis pyrifera*, at Santa Catalina Island, California. Limnol Oceanogr 30:1298–302.
- Zobell CE. 1971. Drift seaweeds on San Diego County beaches. Nova Hedwigia 32:269–314.