

## POSITIVE INDIRECT EFFECTS OF REEF FISHES ON KELP PERFORMANCE: THE IMPORTANCE OF MESOGRAZERS

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**Abstract.** It has been suggested that microcarnivorous reef fishes may play an important role in giant kelp forest communities by preventing infestations of mesograzers that could severely impact or potentially destroy recovering kelp forests after extreme disturbance events. However, these trophic linkages, specifically the direct and indirect effects of fishes on the biomass of mesograzers, grazing intensity, and the performance of giant kelp, have not been sufficiently quantified and evaluated as to their importance and in the absence of such disturbance events. We examined experimentally the effects of mesograzers on the growth and performance of giant kelp in the presence and absence of their fish predators near Santa Catalina Island, California (USA). Mesograzer biomass and grazing intensity were significantly higher when fishes were excluded from giant kelp, which in turn, lowered kelp performance. This pattern was consistent both on experimental plots of kelp as habitat isolates, and on a continuous reef. Moreover, the abundance of mesograzers was inversely related to the abundance of kelp perch among several kelp-forested reefs, suggesting that these effects can occur at larger spatial scales.

Because of differences in the diet and behavior of two microcarnivorous fishes, the kelp perch and señorita, we conducted an experiment manipulating each species and its density independently to determine their separate effects on mesograzers and kelp performance. Concurrently we examined the growth and mortality of juvenile kelp. Grazing intensity decreased, estimates of kelp performance increased, and the growth of juvenile kelp increased with increasing densities of fish but with no detectable effects between fishes. Our results demonstrate that these microcarnivorous fishes have positive indirect effects on kelp performance by reducing mesograzer biomass and grazing intensity, and the early life stages of other fishes also may be important. More specifically, these fishes have a positive effect on the density of fronds of giant kelp that can result in greater recruitment success and the abundance of kelp-associated invertebrates and fishes. Indeed, this study suggests that mesograzers have the potential to be one of the most important herbivores in kelp forest ecosystems.

**Key words:** *Brachyistius frenatus*; *giant kelp*; *grazing*; *indirect effects*; *kelp perch*; *Macrocystis pyrifera*; *mesograzer*; *Oxyjulis californica*; *reef fishes*; *señorita*; *trophic cascades*.

### INTRODUCTION

Food webs represent an important component of community ecology in describing the flow of energy among trophic levels (Paine 1980, Carpenter et al. 1987, Menge 1992, Forrester et al. 1999, Nielsen 2001, Bascompte et al. 2005). By examining relationships between producers and consumers, ecologists have attempted to determine which trophic levels, if removed, may regulate community structure. In several instances, such removals can have “cascading effects” (Carpenter et al. 1985, Polis 1991, 1994, Pace et al. 1999). Predator–prey interactions in food webs remain underlying issues in the study of trophic cascades (e.g., Byrnes et al. 2006), and the outcomes from these interactions can be modified directly and indirectly (Carpenter et al. 1985,

Polis 1994, Menge 1995), yielding positive or negative effects (Abrams 1987). Of particular interest are the relative effects of various herbivores on primary producers (Strauss 1991, Palmisano and Fox 1997, Duffy and Hay 2000, Sessions and Kelly 2001, Sala and Graham 2002).

The importance of trophic cascades has been demonstrated in several marine ecosystems, including kelp forests (Estes 1978), rocky intertidal habitats (Menge 1995), benthic algal communities (Duffy and Hay 2000), salt marshes (Silliman and Bertness 2002), and pelagic environments (Micheli 1999). A classic example is the sea otter–sea urchin–kelp interaction (Estes 1978). Historically, overharvesting of sea otters released sea urchins from predation, which in turn increased herbivory and negatively impacted kelp forests. When populations of sea otters began to recover following laws enacted for their protection, populations of sea urchins decreased, resulting in an increase in the biomass of kelp forests. Estes et al. (1998) later suggested that

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otter populations have suffered another decline due to predation from killer whales; this predation may indirectly result in an increase in populations of sea urchins, which subsequently cause a decrease in the abundance of kelp. Many other studies suggest that the distribution and abundance of kelp forests are determined by processes that regulate the abundance of sea urchins or their grazing behavior (e.g., Leighton et al. 1966, Lawrence 1975, Dayton 1985, Estes and Duggins 1995; for review see Steneck et al. 2002).

Because giant kelp (*Macrocystis pyrifera*) is a major component of rocky reefs throughout the northeastern Pacific and creates a tremendous amount of habitat structure, variation in the presence and abundance of giant kelp (Dayton and Tegner 1984, Dayton 1985, Nisbet and Bence 1989) can have profound effects on nearshore communities (Foster and Schiel 1985, Graham 2004). Giant kelp forests are extremely dynamic but are also well buffered from extinction (Bernstein and Jung 1979) and can readily recover from extreme events such as the El Niño Southern Oscillation (ENSO) (Dayton and Tegner 1984, Tegner and Dayton 1987, Graham 2002, Edwards 2004). Yet despite the resilience of giant kelp forests following disturbance, they also can be severely impacted by macroherbivores (Lawrence 1975, Cowen 1983, Tegner and Dayton 2000, Steneck et al. 2002), which may have long-lasting effects (Ebeling et al. 1985).

The impacts of various amphipods, other small crustaceans, and small gastropods as “mesograzers” (sensu Duffy and Hay 2000) on primary producers also may not be trivial. Such impacts have been documented in seagrass beds (Van Dolah 1978, Kitting et al. 1984, Jernakoff et al. 1996, Duffy et al. 2001, 2005), on benthic algae (Duffy and Hay 2000, Graham 2002), and on coral reefs (Brawley and Adey 1981, Zellar 1988). The potential importance of these herbivores in giant kelp forests has been suggested in the context of extreme ENSO events (Jones 1965, Tegner and Dayton 1987, Graham 2002), whereby the loss of giant kelp and a prolonged period of recovery may be a result of displacement of microcarnivorous kelp-associated fishes (e.g., kelp perch, *Brachyistius frenatus*, and señorita, *Oxyjulis californica*) that feed on mesograzers (Bray and Ebeling 1975, Hobson and Chess 1976, Bernstein and Jung 1979, Coyer 1979). Specifically, the loss of these fishes may release mesograzers from predation, causing severe outbreaks of amphipods that inhibit recruitment and the recovery of giant kelp (Tegner and Dayton 1987, Dayton and Tegner 1989, Graham 2002). Both Jones (1965) and Bernstein and Jung (1979) have implicated the herbivorous isopod *Pentidotea resecta* in inflicting severe damage on the canopy of giant kelp, and Graham (2002) has used “curled” kelp blades as an indicator of the presence of the gammarid amphipod *Ampithoe humeralis*, to derive qualitative estimates of losses in biomass of giant kelp and sporophylls relative to grazing intensity.

Considering the large number of species and high abundance of mesograzers associated with giant kelp (Coyer 1984, 1987), it is surprising that the specific effects of grazing by these species have not received greater attention. Mesograzers in kelp forests may have per capita interaction strengths similar to macroherbivores (Sala and Graham 2002), and because they occur at much higher densities in the field, their potential as significant grazers should not be ignored. Their effects, however, have not been sufficiently quantified experimentally and related to the performance of giant kelp. This lack of information likely stems from the difficulty in developing quantifiable estimates of grazing, testing experimentally the effects of grazing on the performance of kelp, and conducting such tests in nature (Duffy and Hay 2000, Graham 2002).

The objective of our study was to conduct experimental and observational studies in a field setting to determine the effects of mesograzers on the performance of giant kelp, mediated by the presence and density of microcarnivorous fishes. Importantly, we determined whether natural fluctuations in the abundance of mesograzers and their fish predators had measurable effects on the performance of giant kelp in the absence of extreme disturbances such as El Niño. To address these objectives, we asked three questions: (1) what is the biomass of mesograzers in the presence and absence of microcarnivorous reef fishes, and do these fishes have positive indirect effects on the performance of giant kelp?; (2) are the patterns observed on habitat isolates of kelp similar to those observed in a kelp forest on continuous reef and among kelp-forested reefs?; and (3) is mesograzer biomass, grazing intensity, and the performance of giant kelp dependent on the species and density of fish?

## MATERIALS AND METHODS

### *Study system and species*

This study was conducted on the leeward side of Santa Catalina Island, California, near the Wrigley Marine Science Center (WMSC; 33°27' N, 118°29' W), an area with numerous kelp-forested rocky reefs. All experiments were conducted along the south side of Big Fisherman Cove (BFC), an area of sandy bottom bordered by a rocky reef that supports stands of giant kelp. Observational surveys of kelp forests were conducted within a 6 km radius of WMSC.

Microcarnivorous reef fishes in southern California kelp forest ecosystems include, but are not limited to, the kelp perch, *Brachyistius frenatus*, and the señorita, *Oxyjulis californica* (Hubbs and Hubbs 1954, Hobson 1971, Bray and Ebeling 1975, Coyer 1979, Anderson 1994). The kelp perch is a live-bearing embiotocid that feeds on small, motile invertebrates on and around kelp (Hobson 1971, Bray and Ebeling 1975, Coyer 1979), occurring from Vancouver Island, Canada to Baja California (Miller and Lea 1972). The señorita is a generalist predator that ranges from central California

to Baja California and feeds opportunistically on small, motile invertebrates associated with the surface of kelp and the benthos (Hobson 1971, Bray and Ebeling 1975, Bernstein and Jung 1979). Mesograzers, including gammarid amphipods, isopods, gastropods, mysids, and harpacticoid copepods are abundant in southern California kelp forests (Coyer 1984, 1987).

*Mesograzers, microcarnivorous fishes,  
and giant kelp performance*

*Experimental design.*—An experiment in summer 2003 was conducted to determine the effects of mesograzers on the performance of giant kelp in the presence and absence of microcarnivorous fishes. For this experiment, an array of 12 plots of giant kelp was constructed on sandy bottom in a complete randomized block design because of differences in water depth and possibly current flow over a distance of nearly 200 m. The plots were positioned at depths of 5–8 m, with each plot separated from another and a nearby reef by at least 10 m. Each plot consisted of six adult giant kelp translocated from rocky reefs outside of BFC and anchored 1 m from each other in a triangular pattern. Frond heights were standardized to 6 m above the sea floor, and fronds were removed as necessary so that the mean number of fronds per plot was equivalent. Three treatments of four plots each were established: (1) “fish exclusion,” in which reef fishes were excluded from kelp by a pen enclosure; (2) “fish access,” in which reef fishes were allowed access to kelp; and (3) a “cage control,” in which nylon mesh panels interspersed with open areas allowed access to reef fishes. Pen enclosures consisted of a 5 m diameter, 10-mm mesh nylon cylinder extending from the sea floor to the sea surface. The size of mesh used for each pen allowed access to invertebrates but prevented entry by their piscine predators. To address potential caging artifacts (Dayton and Oliver 1980, Steele 1996) on the abundance of mesograzers and kelp performance, three panels of nylon mesh material were placed around each plot that was designated as a cage control. Kelp blades and their associated mesograzers and encrusting epifauna were sampled and quantified, grazing was estimated, and the effects of grazing on kelp were validated (Appendix A). As part of this experiment to monitor any potential differences in natural conditions and our plots of kelp, the invertebrate assemblage on Habitat Reef, an adjacent natural kelp forest, was sampled concurrently.

*Estimates of kelp performance.*—Growth of giant kelp depends upon the concentration of available nitrogen in seawater, its availability with temperature (Gerard 1982, Zimmerman and Kremer 1984), and internal nitrogen reserves that can be used over 2–4 weeks during periods of low nitrogen availability (Gerard 1982). To determine how mesograzers may affect nitrogen allocation in giant kelp, carbon and nitrogen (C:N) concentrations of kelp blades and haptera were determined in each treatment and from kelp at the natural reef. In addition, the

change in frond density, number of growing meristems, blade growth, and haptera growth were recorded as estimates of kelp performance (Appendix B).

*Statistical analyses.*—A one-way blocked analysis of variance (ANOVA) was used to determine if there were significant differences in the biomass of all invertebrates, mesograzers, and encrusting epifauna and in the percentage hole area per surface area of kelp blades (i.e., grazing intensity). If there was no difference among blocks ( $P > 0.25$ ), data were pooled (Underwood 1997) and a one-way ANOVA was used to determine whether there were differences among treatments. A one-way blocked ANOVA was also used to test for differences in parameters of kelp performance, including carbon-to-nitrogen ratios, blade growth, haptera growth, differences in the number of fronds, and the number of meristems. If block effects were nonsignificant as described above, a one-way ANOVA was used to determine whether there were significant differences among treatments. A Cochran's *C* Test was performed prior to all analyses to test the assumption of homogeneity of variances among treatments; when heterogeneous variances were observed, data were log-transformed, after which assumptions were met. When significant differences were detected, a Ryan-Einot-Gabriel-Welsch multiple *F* test (REGWF option, SAS Institute 1999) was used to identify differences among treatments.

*Scaling up: from kelp patches to kelp forests*

To determine whether the results from isolated experimental plots of kelp at smaller spatial scales were similar to those within kelp forests on continuous reef, an experiment was conducted in summer 2004 using the same procedures described in the previous experiment. In this experiment, however, enclosures were placed randomly over selected plots within the kelp forest on Habitat Reef and compared to randomly chosen uncaged plots on the reef. Caged and uncaged plots were paired at the edge, middle, and back of the reef ( $n = 3$  per treatment) in a stratified randomized block design. All plots were standardized by frond density,  $135 \pm 2.0$  fronds per plot (mean  $\pm$  SE), with no differences among plots in the number of fronds per treatment (paired *t* test:  $t = -0.08$ ,  $df = 2$ ,  $P = 0.95$ ). Because there were no detectable artifacts from caging in the previous experiment, cage controls were not employed in this experiment.

Total invertebrate biomass, mesograzer biomass, and kelp blades were collected every two weeks from 13 July to 11 September 2004. These variables and the estimates of kelp performance used in the previous experiment were monitored and quantified with the same methods described earlier, except that encrusting epifauna biomass and haptera growth were not evaluated. Frond growth was monitored as an additional parameter of kelp performance by randomly selecting two newly growing fronds ( $\leq 1$  m) from individual giant kelp on

each plot and tagging each frond with flagging tape 20 cm below the meristem, for a total of 12 fronds per plot. At the end of the experiment, all remaining fronds were collected, and the distance between the tag (with 20 cm subtracted) and the growing meristem was recorded.

To determine if herbivore biomass varied with the abundance of microcarnivorous reef fishes at a larger spatial scale of entire reefs, mesograzers biomass and fish abundance were compared among eight reefs spanning a distance of 10 km. Estimates of the density of kelp perch and señorita were obtained from six random transects (2 m wide  $\times$  2 m high  $\times$  30 m long) conducted in midwater (halfway between the reef bottom and the water surface) at each reef. Four kelp blades and their associated invertebrates were collected from each of four randomly selected giant kelp on two transects for a total of 16 blades collected per reef. Mesograzers were quantified using the methods described previously.

*Statistical analyses.*—Differences in total invertebrate biomass, mesograzers biomass, grazing, C:N ratio, blade growth, frond growth, frond number, and the number of growing meristems were compared between treatments using paired-comparisons *t* tests. For observations among reefs, correlation was used to determine the relationship between the biomass of herbivores and the density of kelp perch and señorita. Because we did not calculate blade area for the blades collected among reefs, invertebrate and mesograzers biomass was standardized to blade mass and not blade area as in the experiments. However, we performed a correlation between blade area and blade mass for 64 blades collected randomly, and determined that blade area is strongly related to blade mass ( $r = 0.80$ ,  $P < 0.0001$ ). To meet the assumption of linearity and homogeneity of variances for correlation analysis, the densities for each species of fish were log-transformed, after which the assumptions were met.

#### *Species- and density-mediated effects of reef fishes*

*Experimental design.*—Because of differences in the diet and behavior of kelp perch and señorita (Bray and Ebeling 1975, Hobson and Chess 1976), an experiment was conducted to investigate whether these two fishes affect mesograzers biomass and kelp performance differentially, and if so, whether these effects are related to their densities. Ten experimental plots of kelp were constructed as described for previous experiments. The number of fronds was standardized among plots ( $142 \pm 2.5$  fronds), with no significant difference in the number of fronds among treatments (one-way ANOVA,  $F_{2,7} = 2.41$ ,  $P = 0.16$ ). Eight plots were surrounded with enclosures (the pens used in previous experiments), and two plots were left uncaged to allow access to all fishes. Adult señorita and kelp perch were captured using a BINCKE net (Anderson and Carr 1998) and placed on enclosed plots at densities of 0, 2, 4, and 8 fish per plot, with each plot containing one species at one level of density. A pilot study conducted in 2003 showed that

kelp perch and señorita placed within pens showed no adverse effects of the pen on their behavior, and there was no mortality of fish over a 30-day period. In the pilot study and during the course of this experiment, both species of fish were observed feeding or “picking” at organisms on the surface of kelp blades.

Kelp blades and associated invertebrates were collected every two weeks from 8 May to 10 July 2004. The parameters of kelp performance were quantified with the same methods described previously. An additional component in this experiment included estimates of growth and mortality of juvenile giant kelp. A total of 120 juvenile kelp were collected from Habitat Reef. Initial surface area and wet mass of juvenile kelp were measured using the same methods described previously. Twelve individuals were attached to the bottom of each of the 10 plots, and the surface area and wet mass of the remaining individuals were measured after six weeks. Mortality was scored only in cases in which the stipe but not blade remained, because we could not ascertain whether missing individuals were actually consumed.

*Statistical analyses.*—Differences in the effects of species and their density on the biomass of all invertebrates and mesograzers, grazing intensity, and kelp performance were determined with analysis of covariance (ANCOVA), with species as the main effect and the density of fish as a covariate. To meet the assumption of homogeneity of variances, data for the biomass of invertebrates, mesograzers, and grazing required log transformations, after which the assumption was met. To evaluate the growth of juvenile kelp and mortality, an ANCOVA model also was used, with species as the main effect and the density of fish as a covariate.

## RESULTS

### *Mesograzers, microcarnivorous fishes, and giant kelp performance*

*Invertebrate biomass and grazing.*—Over 45 days, the biomass of all invertebrates and of mesograzers was significantly higher on plots of kelp in which fishes were excluded than on plots that allowed their access (total invertebrates,  $F_{2,9} = 101.3$ ,  $P < 0.001$ ; Fig. 1A; mesograzers,  $F_{2,9} = 11.4$ ,  $P = 0.003$ ; Fig. 1B). Ten days after removal of enclosures, however, the biomass of all invertebrates and mesograzers in the “fish exclusion” treatment were similar to the other treatments (total invertebrates,  $F_{2,9} = 0.80$ ,  $P = 0.47$ ; Fig. 1A; mesograzers,  $F_{2,9} = 0.74$ ,  $P = 0.50$ ; Fig. 1B). Grazing was significantly higher in the absence of microcarnivorous fishes than in other treatments ( $F_{2,9} = 39.0$ ,  $P < 0.001$ ; Fig. 1C), and the results for presence of fishes and cage controls did not differ in the biomass of all invertebrates, mesograzers, or grazing intensity, and these did not appear to differ from Habitat Reef (Fig. 1A–C). Also, the biomass of encrusting epifauna was not significantly higher within plots that excluded fishes than in plots that allowed their access or in cage controls

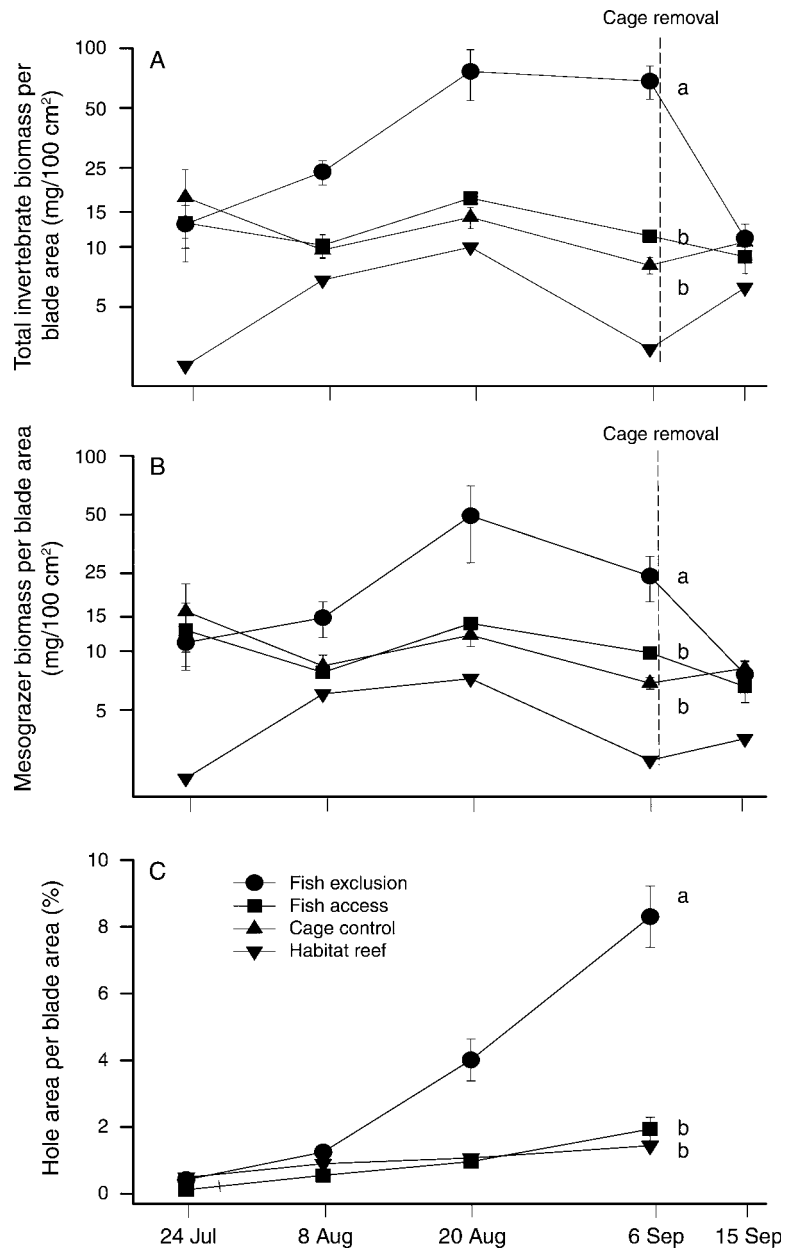


FIG. 1. For the 2003 experiment on kelp habitat isolates examining invertebrate biomass and grazing, the graphs show the change in (A) total invertebrate biomass per blade, (B) mesograzer biomass per blade, and (C) the percentage of hole area per area of blade for three treatments (mean  $\pm$  SE): "fish exclusion," "fish access," and "cage control" and the adjacent natural reef, Habitat Reef (not included in analysis) over a 45-day period in 2003. Pens for the "fish exclusion" and nylon mesh panels for the "cage control" were removed (dashed line) after 45 days. We did not expect a change in grazing intensity (C) after removal of pens; therefore data were not collected to estimate grazing intensity. Treatments with the same lowercase letter are not significantly different from each other. Note the log scale in panels A and B.

( $F_{2,9} = 1.20$ ,  $P = 0.41$ ; Appendix D) and there was  $<2\%$  biomass of encrusting epifauna among all treatments.

Over the five-day experiment to validate grazing effects by mesograzers, there was significantly less blade area ( $t = 5.27$ ,  $df = 22$ ,  $P < 0.001$ ; Appendix C: Fig. C1a) and a greater loss of biomass ( $t = 4.11$ ,  $df = 22$ ,  $P < 0.001$ ; Appendix C: Fig. C1b) when mesograzers were present than absent. Holes in the pieces of kelp blades

were consistent with those observed in field experiments, and this loss of tissue was attributed directly to grazing by mesograzers.

*Kelp performance.*—There was a significant reduction in the number of fronds ( $F_{2,9} = 5.55$ ,  $P = 0.03$ ; Fig. 2A) and significantly fewer meristems ( $F_{2,9} = 26.6$ ,  $P < 0.001$ ; Fig. 2B) on plots in which fishes were excluded than in other treatments. Very little growth of kelp blades ( $<0.5$  mm)

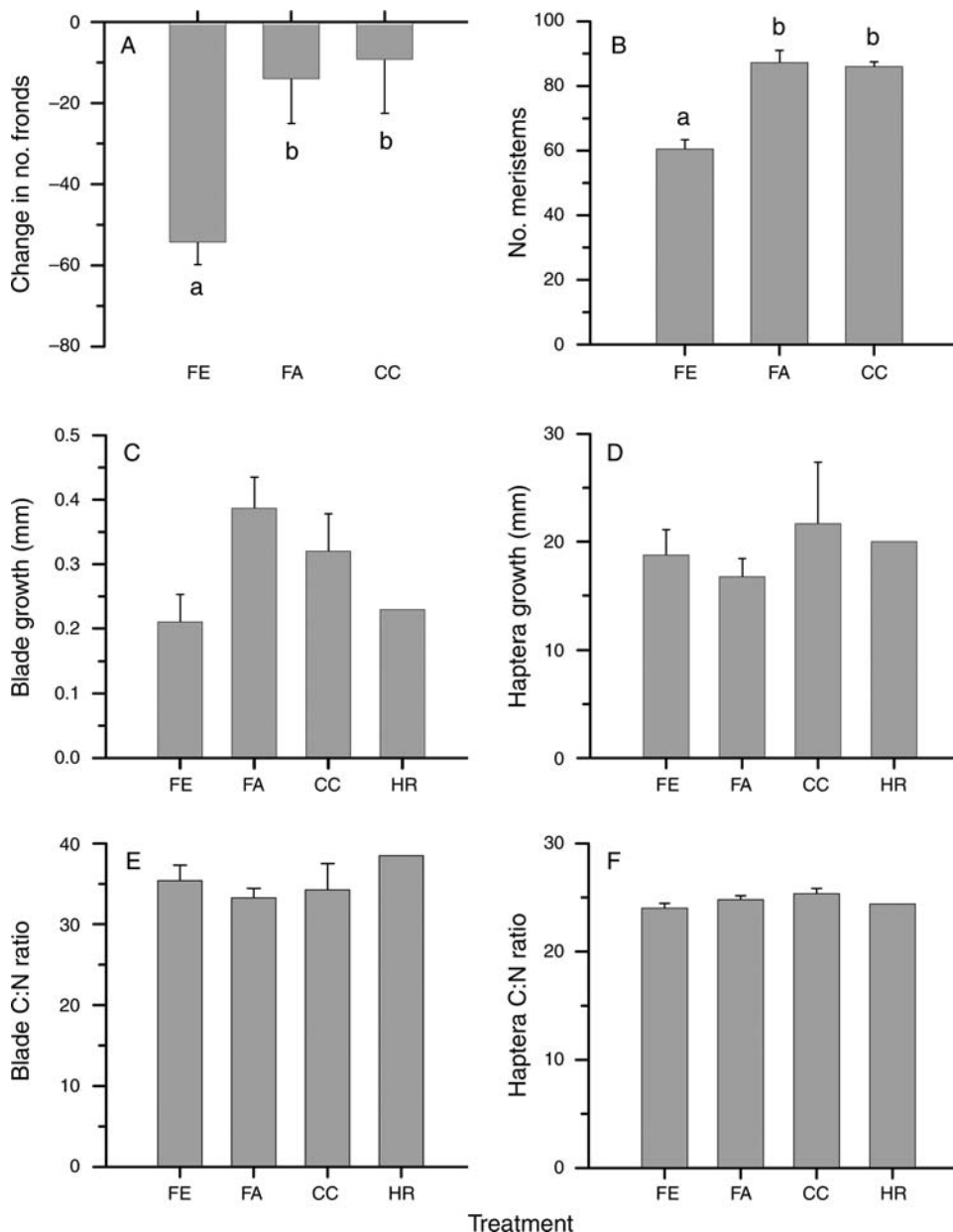


FIG. 2. For the 2003 experiment on kelp habitat isolates, the graphs show the estimates of kelp performance (mean  $\pm$  SE): (A) change in number of fronds, (B) number of growing meristems, (C) growth of blades, (D) growth of haptera, (E) blade C:N ratio, and (F) haptera C:N ratio for each of three treatments: (FE) "fish exclusion," (FA) "fish access," and (CC) "cage control," and Habitat Reef (HR: graphs C–F). The data shown for Habitat Reef are not included in the analyses. Treatments with the same lowercase letter are not significantly different from each other.

occurred, but there was a trend toward lower growth on plots in which fishes were absent ( $F_{2,9} = 3.13$ ,  $P = 0.09$ ; Fig. 2C). There was no difference among treatments in the growth of haptera ( $F_{2,9} = 1.02$ ,  $P = 0.40$ ; Fig. 2D) or in carbon-to-nitrogen ratios for kelp blades ( $F_{2,9} = 0.05$ ,  $P = 0.95$ ; Fig. 2E) and haptera ( $F_{2,9} = 2.05$ ,  $P = 0.14$ ; Fig. 2F). Estimates of kelp performance on plots that allowed access to fishes, including cage controls, were similar to those obtained from Habitat Reef (Fig. 2C–F).

#### Scaling up: from kelp patches to kelp forests

*Invertebrate biomass.*—During the course of this experiment on Habitat Reef, a large pulse of recruitment of kelp bass, *Paralabrax clathratus*, occurred on Habitat Reef between the third and final dates in sampling our treatments, passing through the mesh to occupy plots that were intended to exclude fishes. As many as 100 or more recruits of kelp bass per experimental unit were observed. Recently settled kelp bass are planktivorous,

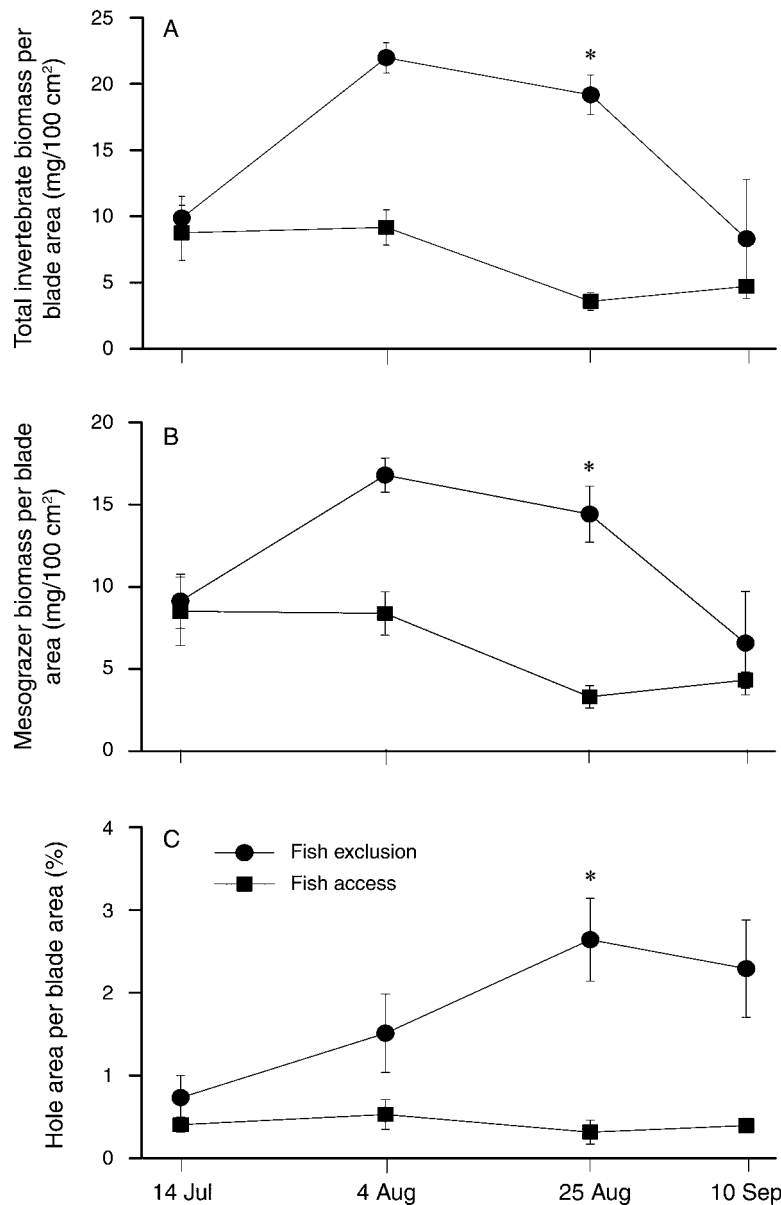


FIG. 3. For the 2004 experiment within a continuous kelp forest examining invertebrate biomass and grazing, the graphs show the change in (A) total invertebrate biomass per blade, (B) mesograzer biomass per blade, and (C) percentage of hole area per area of blade between two treatments (mean  $\pm$  SE): "fish exclusion" and "fish access" within Habitat Reef over 58 days in 2004.

\* Significant difference ( $P < 0.05$ ) between treatments.

but young kelp bass as small as 2 cm in total length feed on kelp-associated invertebrates (M. Carr, *personal communication*), and have the potential to strongly reduce the abundance of mesograzers. As a result, the integrity of our experiment may have been compromised. We chose to analyze the third sampling date as our most unbiased estimate of total invertebrate biomass, mesograzer biomass, and grazing intensity. For this sampling date, there was a significant increase in total invertebrate biomass in the absence of fishes compared to other treatments ( $t = 11.47$ ,  $df = 2$ ,  $P <$

0.01; Fig. 3A). Similarly, mesograzer biomass was significantly higher in the absence of fishes than in other treatments ( $t = 6.79$ ,  $df = 2$ ,  $P = 0.02$ ; Fig. 3B) and this was also true for grazing intensity ( $t = 6.46$ ,  $df = 2$ ,  $P = 0.02$ ; Fig. 3C). The trends in these variables began to converge by the final sampling date (Fig. 3), and at the end of the experiment, total invertebrate biomass, mesograzer biomass, and grazing intensity did not differ among treatments ( $t = 0.86$ ,  $df = 2$ ,  $P = 0.48$ ; Fig. 3A,  $t = 0.80$ ,  $df = 2$ ,  $P = 0.51$ ; Fig. 3B,  $t = 2.95$ ,  $df = 2$ ,  $P = 0.10$ ; Fig. 3C), respectively.

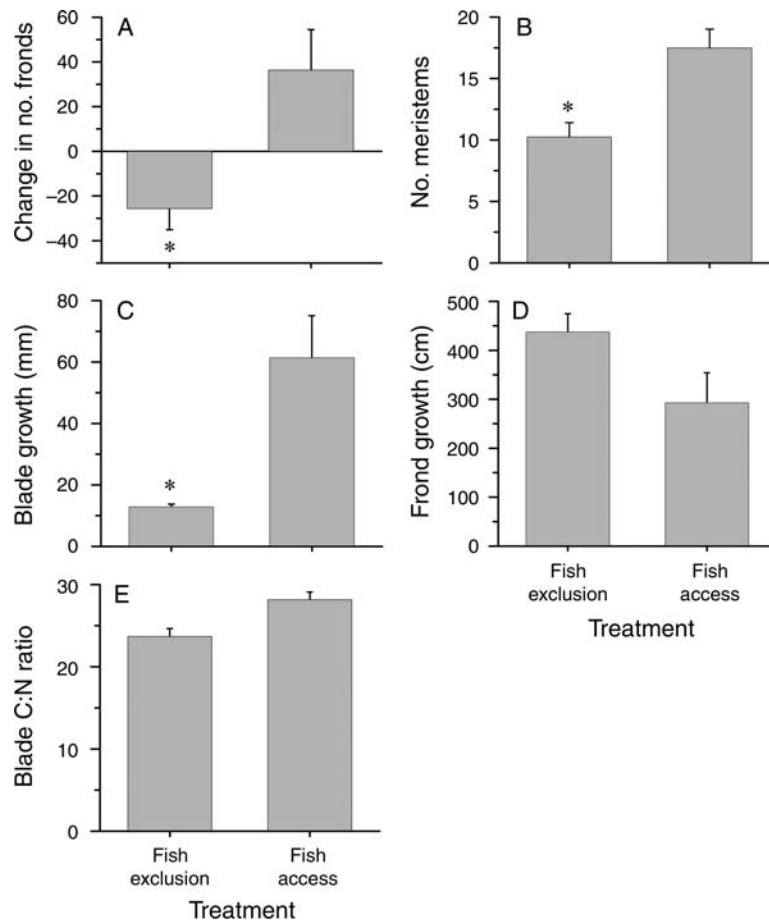


FIG. 4. For the 2004 experiment within a continuous kelp forest, the graphs show the estimates of kelp performance (mean  $\pm$  SE): (A) change in fronds, (B) number of growing meristems, (C) growth of blades, (D) growth of fronds, and (E) blade C:N ratio between two treatments: "fish exclusion" and "fish access" within Habitat Reef.

\* Significant difference ( $P < 0.05$ ) between treatments.

*Kelp performance.*—There was a significant difference in the change in number of fronds on plots in which fishes were absent than present ( $t = 4.13$ ,  $df = 2$ ,  $P = 0.05$ ; Fig. 4A), with fewer numbers of growing meristems ( $t = 18.57$ ,  $df = 2$ ,  $P = 0.003$ ; Fig. 4B) in treatments that excluded fishes. The growth of kelp blades was higher when fishes were present ( $t = 5.87$ ,  $df = 2$ ,  $P = 0.03$ ; Fig. 4C), but there was no difference in the growth of fronds ( $t = 1.51$ ,  $df = 2$ ,  $P = 0.27$ ; Fig. 4D) or in carbon-to-nitrogen ratios of kelp blades ( $t = 3.09$ ,  $df = 2$ ,  $P = 0.09$ ; Fig. 4E) between treatments.

*Relationships among reefs.*—There was a significant negative correlation between mesograzer biomass and the density of fish among eight reefs within a distance of  $\sim 10$  km for kelp perch ( $r = -0.75$ ,  $P = 0.03$ ; Appendix E: Fig. E1a), but not señorita ( $r = 0.08$ ,  $P = 0.85$ ; Appendix E: Fig. E1b). For señorita, the densities of fish were very low, except for one reef.

#### *Species- and density-mediated effects of reef fishes*

*Invertebrate biomass.*—There were no differences in the biomass of all invertebrates and mesograzers

between species of fish (total invertebrates,  $F_{1,7} = 0.57$ ,  $P = 0.49$ ; Fig. 5A; mesograzers,  $F_{1,7} = 0.24$ ,  $P = 0.65$ ; Fig. 5B) or significant interactions between species and their density (total invertebrates,  $F_{1,7} = 1.18$ ,  $P = 0.34$ ; mesograzers,  $F_{1,7} = 0.17$ ,  $P = 0.34$ ). The density of fish marginally reduced the total biomass of invertebrates ( $F_{1,7} = 7.09$ ,  $P = 0.06$ ; Fig. 5A) and mesograzers ( $F_{1,7} = 6.70$ ,  $P = 0.06$ ; Fig. 5B). At a density of four fish per plot, a reduction in the biomass of all invertebrates and mesograzers was apparent. Grazing was not affected by species of fish ( $F_{1,7} = 0.86$ ,  $P = 0.39$ ; Fig. 5C), and there was no interaction between species and their density ( $F_{1,7} = 0.62$ ,  $P = 0.43$ ). Higher densities of fish resulted in less grazing ( $F_{1,7} = 12.08$ ,  $P = 0.01$ ,  $r^2 = 0.68$ ; Fig. 5C), and a density of four or more kelp perch per plot showed a visible reduction in grazing intensity.

*Kelp performance.*—For all estimates of kelp performance, there was no significant effect of fish species ( $P \geq 0.30$ ; Fig. 6A–E) or interactions between species and their density ( $P \geq 0.06$ ; Fig. 6A–E). The density of fish was related to the number of meristems ( $F_{1,7} = 9.14$ ,  $P = 0.03$ ; Fig. 6B) and marginally related to the growth of

kelp blades ( $F_{1,7}=6.06$ ,  $P=0.06$ ; Fig. 6C), but not to the change in number of fronds ( $F_{1,7}=3.09$ ,  $P=0.14$ ; Fig. 6A), frond growth ( $F_{1,7}<0.001$ ,  $P=0.99$ ; Fig. 6D), or the carbon-to-nitrogen ratio of kelp blades ( $F_{1,7}=0.84$ ,  $P=0.36$ ; Fig. 6E).

*Growth and mortality of juvenile giant kelp.*—There was no effect of fish species on the growth of juvenile kelp, but there was a significant effect of the density of fish (ANCOVA; species,  $F_{1,7}=0.001$ ,  $P=0.98$ ; density,  $F_{1,7}=16.55$ ,  $P<0.001$ ,  $r^2=0.36$ ; species  $\times$  density interaction,  $F_{1,7}=0.001$ ,  $P=0.99$ ; Appendix F: Fig. F1a). Mortality of juvenile kelp was not affected by fish species or density (ANCOVA; species,  $F=0.08$ ,  $P=0.78$ ; density,  $F_{1,7}=1.96$ ,  $P=0.22$ ; species  $\times$  density interaction,  $F_{1,7}=0.82$ ,  $P=0.42$ ; Appendix F: Fig. F1b), but mortality was noticeably higher in the absence of reef fishes.

#### DISCUSSION

Herbivory by macroinvertebrates may cause deforestation and extinction of kelp forests, and grazing by sea urchins and carnivory by predators of sea urchins may determine how consumers structure species interactions (reviewed by Steneck et al. 2002). Considering the prevalence of mesograzers in giant kelp forests (Coyer 1984, Tegner and Dayton 1987) and their potential to exert strong negative effects, the importance of their impacts is just now being realized (Graham 2002, Sala and Graham 2002). Our results clearly demonstrate the impacts of mesograzers in a giant kelp forest ecosystem. When released from predation by fishes, mesograzers increase dramatically over 2–4 weeks, and despite their small size, have measurable negative effects on kelp performance and the growth and possibly mortality of juvenile giant kelp. Such increases over much longer periods have the potential to greatly reduce or destroy entire kelp forests following major ENSO events (Jones 1965, Tegner and Dayton 1987, Graham 2002). In the absence of severe disturbances such as El Niño or major storm activity that may affect the recovery of kelp forests through subsequent herbivory, however, it is clear that mesograzers have significant impacts on giant kelp without such events. In the absence of or with lower densities of fishes that reduce mesograzers, giant kelp suffers an increase in grazing severity that results in lower kelp performance, including reduced growth of blades and a reduction in the number of fronds and meristems.

One issue in conducting this study using habitat isolates that are more amenable to experimentation is whether the observed effects are relevant at much larger areas of habitat commonly found in nature (e.g., Carr et al. 2002). Because microcarnivorous fishes vary in density within and among reefs of giant kelp (e.g., Carr 1994, Anderson 1994), they may not appreciably reduce large numbers of mesograzers on continuous reefs at low densities. Alternatively, at higher densities, fishes may exhibit stronger effects, and negative impacts on giant kelp may not be revealed. In comparing the results from

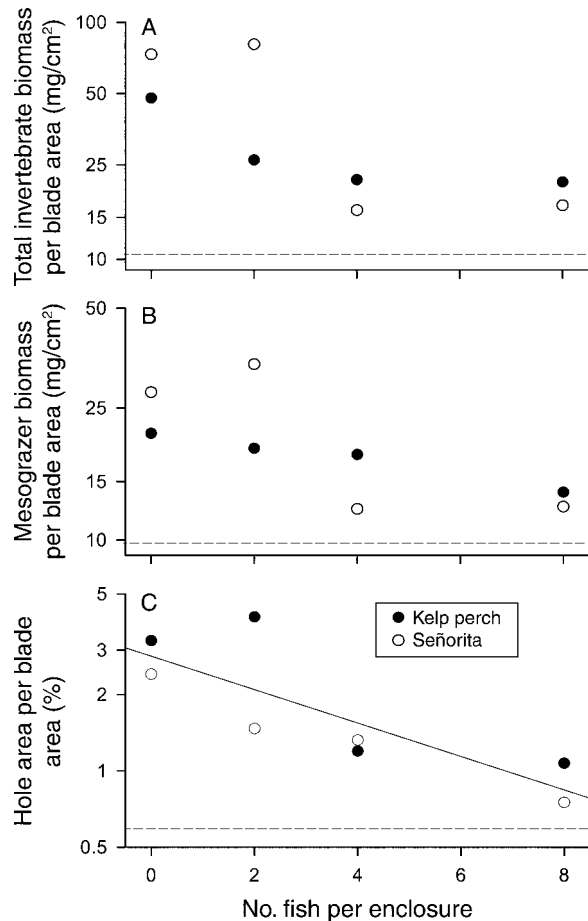


FIG. 5. Relationship between (A) total invertebrate biomass, (B) mesograzer biomass, and (C) percentage hole area per blade and the density of señorita and kelp perch. Dashed lines represent the mean value of two plots of kelp that allowed full access to fishes. Note the log scales for the y-axes.

our separate experiments on isolated plots of kelp and with equivalent plots on a continuous reef, increases in the abundance of mesograzers and impacts on giant kelp were consistent between experiments. For the experiment on continuous reef, however, a decline in the biomass of invertebrates and grazing intensity on plots that excluded fishes was observed at the completion of the experiment. This decline is similar to the one observed in the first experiment with isolated plots of giant kelp after the pens used to exclude fishes were removed. We attribute the decline in mesograzers and grazing intensity on continuous reef to a large recruitment pulse of kelp bass, *Paralabrax clathratus*, which occurred in July 2004 at Habitat Reef. It is likely that these kelp bass were responsible for the decline in mesograzers during the latter part of this experiment, but the increase in mesograzers and their negative effects on kelp performance were clearly evident before the completion of the experiment. The general importance of mesograzers and their predators is further supported

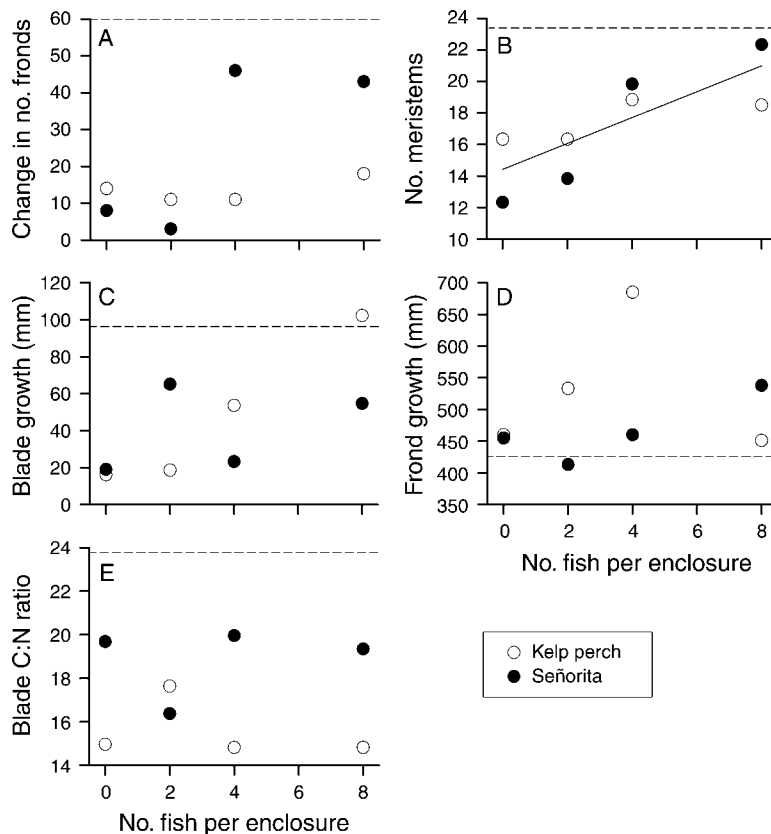


FIG. 6. Relationship between estimates of kelp performance and the density of kelp perch and señorita: (A) change in fronds, (B) number of growing meristems, (C) growth of blades, (D) growth of fronds, (E) blade C:N ratios. Dashed lines represent the mean value of two plots of kelp that allowed full access to fishes.

by the inverse relationship between the density of kelp perch and the biomass of mesograzers observed among reefs over several kilometers, suggesting that the patterns we observed experimentally are relevant at much larger spatial scales. One reason that an inverse relationship between the biomass of mesograzers and the density of señorita may not have been detected, is that the densities of señorita were low at most reefs.

Despite differences in diet and behavior between the kelp perch and señorita (Bray and Ebeling 1975, Hobson and Chess 1976), these species do not appear to have differential effects on the general abundance of mesograzers or on the performance of giant kelp. Yet in both cases, the densities of these fishes are negatively related to the biomass of mesograzers and grazing intensity. As a result, kelp performance is positively related or nearly so to the density of fish in most cases, and appreciable declines in the biomass of invertebrates and grazing intensity is realized by a density of about four or more fish per 100 m<sup>3</sup>.

The densities of fish relative to their absence or their presence in ambient conditions provides an estimate of relative impacts on mesograzers. Calculations of per capita interaction strength (Sala and Graham 2002, Bascompte et al. 2005) provide a more in-depth

examination of the strength of trophic relationships, and mesograzers on kelp may have similar per capita interaction strengths as macroherbivores that may cause greater impacts on kelp forests because of their much higher densities (Sala and Graham 2002). The information required (e.g., diet, rates of consumption, proportion of prey biomass consumed per capita biomass of the predator) to determine relative per capita interaction strengths would constitute a logical next step in future work to evaluate in more detail the per capita interaction strengths of fishes on mesograzers and in turn, mesograzers on kelp.

The relative importance of different herbivores on primary producers is also of great interest in terrestrial ecosystems. Grazing vertebrates can severely defoliate mistletoe but only affect 32% of the population, while insects cause only a 16% reduction in leaf area but affect 100% of the population (Sessions and Kelly 2001). Insects can cause much greater damage to trees than grazing vertebrates (Strauss 1991), whereas macrograzers can strongly affect the population dynamics of other plants, and insects have only moderate impacts (Palmisano and Fox 1997). An important aspect of trophic interactions in any ecosystem is variability in the abundance of different herbivores and their consump-

tion rate, both of which can be used to calculate their relative impacts (Bascompte et al. 2005).

Three parameters of kelp performance that appear to be unaffected by the presence or absence of fishes and the abundance of mesograzers are carbon-to-nitrogen ratios, the growth of fronds, and the growth of haptera. The lack of differences for these parameters but differences in the growth of blades and the number of fronds and meristems may represent differential allocation of resources. Removal of the canopy of giant kelp can result in an increase in the growth of kelp but a decrease in the production of sporophylls (Reed 1987), and there may be a trade-off between the growth of fronds and reproduction (Graham 2002). The results of our study suggest that the number of fronds and meristems may be more appropriate parameters of kelp performance. If giant kelp increases in growth in response to grazing (Graham 2002), one might expect that treatments with higher abundances of mesograzers and higher grazing intensity would respond accordingly. Such responses did not occur in this study, possibly because most of our experiments were conducted in late spring and summer, a period of low growth due to lower nitrogen concentrations. It is difficult to determine the relative responses of growth in relation to grazing intensity, because we effectively examined their net effects and may have underestimated both factors. Giant kelp may expend its nitrogen reserves in 2–4 weeks (Gerard 1982) in somatic growth to compensate for losses from grazing, and increased grazing during periods of low nitrogen concentration, as in this study, may overwhelm the ability of giant kelp to respond by an increase in the rate of growth. In contrast, Graham (2002) conducted his study in summer but during La Niña conditions (M. Graham, *personal communication*), a period of low temperatures and high nutrient availability that should provide favorable conditions for higher growth (Dayton et al. 1999, Edwards 2004).

Given our results, are the changes in kelp performance that we observed biologically significant in the context of kelp forest community dynamics? Certainly the top-down effects caused by these fishes may indirectly increase the abundance of giant kelp, an important habitat for many invertebrates and fishes (Foster and Schiel 1985, Stephens et al. 2006), and the presence and density of kelp strongly influence the distribution and abundance of fishes (reviewed by Stephens et al. 2006). More specifically, mesograzers-mediated reductions in the density of fronds and blade growth of giant kelp that contribute to lower biomass and structural complexity can have important effects on recruitment of fishes and their abundance in kelp forests, including the effects of kelp as a refuge from predators (Anderson 2001, Johnson 2006). The density of fronds of giant kelp and its relationship to kelp canopy cover and biomass strongly influences recruitment success of rockfishes (Carr 1991), kelp perch (Anderson 1994), and kelp bass (Carr 1994), species that happen to feed on these

mesograzers (Coyer 1979, Singer 1985; M. Carr, *unpublished data*). Variability in the density of giant kelp fronds also has the potential to affect kelp-associated macroinvertebrates. For example, kelp fronds provide a refuge for snails (*Tegula* spp.) that reduces predator-induced mortality compared with mortality if snails were on the sea floor (Watanabe 1984). The snail *Norrissia norrissi* feeds on giant kelp and also may be protected from predators in this habitat (Wakefield and Murray 1998).

Mesograzers also likely affect the community structure in kelp forests, as they do in other marine ecosystems (reviewed by Duffy and Hay 2000, Duffy et al. 2001, 2005). Higher abundances of mesograzers, followed by a reduction in the biomass of giant kelp and possibly higher mortality of juvenile kelp may increase the amount of space and incident light in kelp forests, which in turn allow for the growth of understory algae. Changes in the community composition of algae (Reed and Foster 1984) can affect the species composition of fishes, resulting in an increase in the abundance of fishes associated with understory algae (Carr 1989, Schmitt and Holbrook 1990). In addition, the effects of predator diversity also have the potential to lower per capita grazing pressure on giant kelp (Byrnes et al. 2006). Whether different species of fishes feed differentially on species of mesograzers, affecting their diversity and species composition, in turn translating into differential grazing pressure on giant kelp, remains to be explored.

This study provides direct evidence that mesograzers reduce kelp performance, with their effects mediated by the presence and density of microcarnivorous fishes. The density of fishes used in this study (1.80–7.33 fish/100 m<sup>3</sup>) are similar and within the natural range of the density of kelp perch and señorita in nature. At 24 kelp-forested reefs surveyed across southern California in 2004, densities of kelp perch and señorita varied from 0.06 to 6.98 fish/100 m<sup>3</sup> and from 1.5 to 72.5 fish/100 m<sup>3</sup>, respectively (California Department of Fish and Game 2006). Thus, the relative abundance and presence of these fishes in kelp forests appears to be important not only after major disturbances in the recovery of giant kelp (e.g., Tegner and Dayton 1987), but also in positively influencing the general overall “health” of kelp forests. Future research concerning the relative importance of different predators on mesograzers, how mesograzers may differentially affect primary producers, and whether these organisms affect the allocation of resources of primary producers in response to grazing intensity, is necessary to further evaluate the relative importance of mesograzers in marine ecosystems.

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## LITERATURE CITED

- Abrams, P. A. 1987. Indirect interactions between species that share a predator: varieties of indirect effects. Pages 38–54 in W. C. Kerfoot and A. Sih, editors. *Predation: direct and indirect impacts on aquatic communities*. University Press of New England, Hanover, New Hampshire, USA.
- Anderson, T. W. 1994. Role of macroalgal structure in the distribution and abundance of a temperate reef fish. *Marine Ecology Progress Series* 113:279–290.
- Anderson, T. W. 2001. Predator responses, prey refuges, and density-dependent mortality of a marine fish. *Ecology* 82: 245–257.
- Anderson, T. W., and M. H. Carr. 1998. BINCKE: a highly efficient net for collecting reef fishes. *Environmental Biology of Fishes* 51:111–115.
- Bascompte, J., C. J. Melian, and E. Sala. 2005. Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences* 102: 5443–5447.
- Bernstein, B. B., and N. Jung. 1979. Selective pressures and coevolution in a kelp canopy community in southern California. *Ecological Monographs* 49:335–355.
- Brawley, S. H., and W. H. Adey. 1981. The effect of micrograzers on algal community structure in a coral reef microcosm. *Marine Biology* 61:167–177.
- Bray, R. N., and A. W. Ebeling. 1975. Food, activity, and habitat of three “picker type” microcarnivorous fishes in the kelp forests off Santa Barbara, California. *United States Fishery Bulletin* 73:815–829.
- Byrnes, J., J. J. Stachowicz, K. M. Hultgren, A. R. Hughes, S. V. Olyarnik, and C. S. Thornber. 2006. Predator diversity strengthens trophic cascades in kelp forests by modifying herbivore behavior. *Ecology Letters* 8:61–71.
- California Department of Fish and Game. 2006. *Compilation and analysis of CIAP nearshore survey data*. Pages C1–C147 in Draft report, Appendix C. California Department of Fish and Game, Sacramento, California, USA.
- Carpenter, S. R., J. Kitchell, and J. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35: 634–639.
- Carpenter, S. R., J. Kitchell, J. Hodgson, P. Cochran, J. Elser, M. Elser, D. Lodge, D. Kretchmer, X. He, and C. Von Ende. 1987. Regulation of lake primary productivity by food web structure. *Ecology* 68:1863–1867.
- Carr, M. H. 1989. Effects of macroalgal assemblages on the recruitment of young-of-the-year rockfishes. *Journal of Experimental Marine Biology and Ecology* 126:59–67.
- Carr, M. H. 1991. Habitat selection and recruitment of an assemblage of temperate zone reef fishes. *Journal of Experimental Marine Biology and Ecology* 146:113–137.
- Carr, M. H. 1994. Effects of macroalgal dynamics on recruitment of a temperate reef fish. *Ecology* 75:1320–1333.
- Carr, M. H., T. W. Anderson, and M. A. Hixon. 2002. Biodiversity, population regulation, and the stability of coral-reef fish communities. *Proceedings of the National Academy of Sciences* 99:11241–11245.
- Cowen, R. K. 1983. The effect of sheephead (*Semicossyphus pulcher*) predation on Red Sea urchin populations: an experimental analysis. *Oecologia* 58:249–255.
- Coyer, J. A. 1979. The invertebrate assemblage associated with *Macrocystis pyrifera* and its utilization as a food source by kelp forest fishes. Dissertation. University of Southern California, Los Angeles, California, USA.
- Coyer, J. A. 1984. The invertebrate assemblage associated with giant kelp, *Macrocystis pyrifera*, at Santa Catalina Island, California: a general description with emphasis on amphipods, copepods, mysids, and shrimps. *Fishery Bulletin* 82:55–66.
- Coyer, J. A. 1987. The mollusk assemblage associated with giant kelp, *Macrocystis pyrifera*, at Santa Catalina Island, California. *Bulletin of the Southern California Academy of Sciences* 83:129–138.
- Dayton, P. K. 1985. Ecology of kelp communities. *Annual Review of Ecology and Systematics* 16:215–245.
- Dayton, P. K., and J. S. Oliver. 1980. An evaluation of experimental analysis of population and community patterns in benthic marine environments. Pages 93–120 in K. Tenore and B. C. Coull, editors. *Marine benthic dynamics*. University of South Carolina Press, Columbia, South Carolina, USA.
- Dayton, P. K., and M. J. Tegner. 1984. Catastrophic storms, El Niño, and patch stability in a southern California kelp community. *Science* 224:283–285.
- Dayton, P. K., and M. J. Tegner. 1989. Bottoms beneath troubled waters: benthic impacts of the 1982–1984 El Niño in the temperate zone. Pages 433–472 in P. W. Glynn, editor. *Global consequences of the 1982–83 El Niño-southern Oscillation*. Elsevier Sciences, Miami, Florida, USA.
- Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1999. Temporal and spatial scales of kelp demography: the role of oceanographic climate. *Ecological Monographs* 69: 219–250.
- Duffy, J. E., and M. E. Hay. 2000. Strong impacts of grazing amphipods on the organization of a benthic community. *Ecological Monographs* 70:237–263.
- Duffy, J. E., K. S. Macdonald, J. M. Rhode, and J. D. Parker. 2001. Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. *Ecology* 82: 2417–2434.
- Duffy, J. E., J. P. Richardson, and K. E. France. 2005. Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. *Ecology Letters* 8:301–309.
- Ebeling, A. W., D. R. Laur, and R. J. Rowley. 1985. Severe storm disturbances and reversal of community structure in a southern California kelp forest. *Marine Biology* 84:287–294.
- Edwards, M. S. 2004. Estimating scale-dependency in disturbance impacts: El Niños and giant kelp forests in the northeast Pacific. *Oecologia* 138:436–447.
- Estes, J. A. 1978. Sea otter predation and community organization in the western Aleutian Islands, Alaska. *Ecology* 59:822–833.
- Estes, J. A., and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecological Monographs* 65:75–100.
- Estes, J. A., M. T. Tinker, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and near shore ecosystems. *Science* 282:473–476.
- Forrester, G. E., T. L. Dudley, and N. B. Grimm. 1999. Trophic interactions in open systems: effects of predators and nutrients on stream food chains. *Limnology and Oceanography* 44:1187–1197.
- Foster, M. S., and D. R. Schiel. 1985. The ecology of giant kelp forests in California: a community profile. U.S. Fish and Wildlife Service Biology Report 85, U.S. Fish and Wildlife Service, Washington, D.C., USA.
- Gerard, V. A. 1982. Growth and utilization of internal nitrogen reserves by the giant kelp, *Macrocystis pyrifera* in a low-nitrogen environment. *Marine Biology* 66:27–35.
- Graham, M. H. 2002. Prolonged reproductive consequences of short-term biomass loss in seaweeds. *Marine Biology* 140: 901–911.
- Graham, M. H. 2004. Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. *Ecosystems* 7:341–357.

- Hobson, E. S. 1971. Cleaning symbiosis among California inshore fishes. *Fishery Bulletin* 69:491–523.
- Hobson, E. S., and J. R. Chess. 1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. *Fishery Bulletin* 74:567–598.
- Hubbs, C. L., and L. C. Hubbs. 1954. Data on the life history, variation, ecology, and relationships of the kelp perch, *Brachyistius frenatus*, an embiotocid fish of the Californias. *California Fish and Game* 40:183–193.
- Jernakoff, P., A. Brearley, and J. Nielson. 1996. Factors affecting grazer-epiphyte interactions in a temperate seagrass meadow. *Oceanography and Marine Biology Annual Review* 34:109–162.
- Johnson, D. W. 2006. Predation, habitat complexity, and variation in density-dependent mortality of temperate reef fishes. *Ecology* 87:1179–1188.
- Jones, L. G. 1965. Canopy grazing at southern Point Loma. Pages 62–63 in W. M. Keck, editor. *Kelp Habitat Improvement Project Annual Report, 1 February 1964–31 March 1965*. Laboratory of Environmental Health and Engineering, California Institute of Technology, Pasadena, California, USA.
- Kitting, C. L., B. Frey, and M. D. Morgan. 1984. Detection of inconspicuous epiphytic algae supporting food webs in seagrass meadows. *Oecologia* 62:145–149.
- Lawrence, J. M. 1975. On the relationships between marine plants and sea urchins. *Oceanography and Marine Biology Annual Review* 13:213–286.
- Leighton, D. L., L. G. Jones, and W. North. 1966. Ecological relationship between giant kelp and sea urchins in southern California. Pages 141–153 in E. G. Young and J. L. McLachlan, editors. *Proceedings of the Fifth International Seaweed Symposium*. Pergamon Press, Oxford, UK.
- Menge, B. A. 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores? *Ecology* 73:755–765.
- Menge, B. A. 1995. Indirect effects in marine intertidal interaction webs: patterns and importance. *Ecological Monographs* 65:21–74.
- Micheli, F. 1999. Eutrophication, fisheries, and consumer resource dynamics in marine pelagic ecosystems. *Science* 285:1396–1398.
- Miller, D. J., and R. N. Lea. 1972. Guide to coastal marine fishes of California. *California Fish Bulletin* 157, California Department of Fish and Game, Sacramento, California, USA.
- Nielsen, K. J. 2001. Bottom-up and top-down forces in tide pools: test of a food chain model in an intertidal community. *Ecological Monographs* 72:187–217.
- Nisbet, R. M., and R. J. Bence. 1989. Alternative dynamic regimes for canopy-forming kelp: a variant on density-vague population regulation. *American Naturalist* 134:377–408.
- Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchel. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* 14:235–240.
- Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* 49: 667–685.
- Palmisano, S., and L. R. Fox. 1997. Effects of mammal and insect herbivory on population dynamics of a native Californian thistle, *Cirium occidentale*. *Oecologia* 111:413–421.
- Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food web theory. *American Naturalist* 138:123–155.
- Polis, G. A. 1994. Food webs, trophic cascades and community structure. *Australian Journal of Ecology* 19:121–136.
- Reed, D. C. 1987. Factors affecting the production of sporophylls in the giant kelp *Macrocystis pyrifera*. *Journal of Experimental Marine Biology and Ecology* 113:61–69.
- Reed, D. C., and M. S. Foster. 1984. The effects of canopy shading on algal recruitment and growth in a giant-kelp forest. *Ecology* 65:937–948.
- Sala, E., and M. H. Graham. 2002. Community-wide distribution of predator-prey interaction strength in kelp forests. *Proceedings of the National Academy of Sciences* 99:3678–3683.
- SAS Institute. 1999. *SAS/STAT user's guide, version 8*. SAS Institute, Cary, North Carolina, USA.
- Schmitt, R. J., and S. J. Holbrook. 1990. Contrasting effects of giant kelp on dynamics of surfperch populations. *Oecologia* 84:2714–2729.
- Sessions, L. A., and D. Kelly. 2001. Heterogeneity in vertebrate and invertebrate herbivory and its consequences for New Zealand mistletoes. *Austral Ecology* 26:571–581.
- Silliman, B. R., and M. D. Bertness. 2002. A trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Sciences* 99:10500–10505.
- Singer, M. 1985. Food habits of juvenile rockfishes (*Sebastes*) in a central California kelp forest. *United States Fishery Bulletin* 83:31–41.
- Steele, M. A. 1996. Effects of predators on reef fishes: separating cage artifacts from effects of predation. *Journal of Experimental Marine Biology and Ecology* 198:249–267.
- Steneck, R. S., M. H. Graham, B. J. Bourque, D. Corbett, J. M. Erlandson, J. A. Estes, and M. J. Tegner. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and their future. *Environmental Conservation* 29:436–459.
- Stephens, J. S., R. J. Larson, and D. J. Pondella. 2006. Rocky reefs and kelp forests. Pages 227–252 in L. G. Allen, D. J. Pondella, and M. H. Horn, editors. *Ecology of marine fishes: California and adjacent waters*. University of California Press, Los Angeles, California, USA.
- Strauss, S. Y. 1991. Direct, indirect, and cumulative effects of three native herbivores on a shared host plant. *Ecology* 72: 543–558.
- Tegner, M. J., and P. K. Dayton. 1987. El Niño effects on southern California kelp forest communities. *Advances in Ecological Research* 17:243–279.
- Tegner, M. J., and P. K. Dayton. 2000. Ecosystem effects of fishing in kelp forest communities. *Journal of Marine Science* 57:579–589.
- Underwood, A. J. 1997. *Experiments in ecology*. Cambridge University Press, London, UK.
- Van Dolah, R. F. 1978. Factors regulating the distribution and population dynamics of the amphipod *Gammarus palustris* in an intertidal salt marsh community. *Ecological Monographs* 48:191–217.
- Wakefield, R. L., and S. N. Murray. 1998. Factors influencing food choice by the seaweed-eating marine snail *Norrisia norrisi* (Trochidae). *Marine Biology* 130:631–642.
- Watanabe, J. M. 1984. The influence of recruitment, competition, and benthic predation on spatial distributions of three species of kelp forest gastropods (Trochidae: *Tegula*). *Ecology* 65:920–936.
- Zellar, D. C. 1988. Short-term effects of territoriality of a tropical damselfish and exclusion of large fishes on invertebrates in algal turfs. *Marine Ecology Progress Series* 44:85–93.
- Zimmerman, R. C., and J. N. Kremer. 1984. Episodic nutrient supply to a kelp forest ecosystem in southern California. *Journal of Marine Research* 42:591–604.

**APPENDIX A**

Procedures for sampling kelp blades, mesograzers, and encrusting epifauna, obtaining estimates of grazing intensity, and validating grazing effects, and a table reporting the taxonomic composition of invertebrates collected from kelp blades (*Ecological Archives* E088-093-A1).

**APPENDIX B**

Procedures for evaluating estimates of kelp performance (*Ecological Archives* E088-093-A2).

**APPENDIX C**

A figure showing results of grazing validation experiment (*Ecological Archives* E088-093-A3).

**APPENDIX D**

A figure showing the biomass of encrusting epifauna among treatments (*Ecological Archives* E088-093-A4).

**APPENDIX E**

A figure showing variation in mesograzer biomass and density of fishes (*Ecological Archives* E088-093-A5).

**APPENDIX F**

A figure showing growth and mortality of juvenile kelp (*Ecological Archives* E088-093-A6).