

EFFECT OF GIANT KELP ON LOCAL ABUNDANCE OF REEF FISHES: THE IMPORTANCE OF ONTOGENETIC RESOURCE REQUIREMENTS

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ABSTRACT

The size and structure of populations of many rocky inshore fishes in southern California, USA, can be profoundly influenced by the canopy-forming giant kelp, *Macrocystis pyrifera*. Forests of giant kelp undergo substantial spatial and temporal variation which in turn can influence the local (among-reef) abundance of substrate-oriented fishes. The effects of kelp are strongly related to the resources required by different life history stages of fishes. Giant kelp has a positive, direct effect on local abundances of species that use it as a nursery ground and/or adult habitat. Kelp can also indirectly affect abundances of fish. These indirect effects, which can be positive or negative, result from the shading of understory algae by kelp. Reef fishes with similar ontogenetic resource requirements appear to share a common relationship with the presence and density of kelp.

Here we explore the relationship between spatial variation in giant kelp (*Macrocystis pyrifera*) and the density of local populations of rocky inshore fish species in the southern California bight, USA. Variation in giant kelp may have profound consequences because giant kelp is the major algal structure on rocky reefs in the bight, providing substrate-oriented fish with a spatial refuge from predators (Ebeling et al., 1980a; 1980b; Ebeling and Laur, 1985), food derived from enhanced secondary productivity (Coyer, 1979), and foraging habitat (Coyer, 1979; Holbrook and Schmitt, 1984). Forests of giant kelp may serve as settlement sites and "nursery" areas for young-of-year fish (Leaman, 1976; Carr, 1989; DeMartini and Roberts, 1990), and habitat for older life stages (Coyer, 1979; Larson and DeMartini, 1984; Carr, 1989; DeMartini and Roberts, 1990).

Giant kelp forests off California vary in space and time (Coyer, 1979; Dayton et al., 1984; Dayton, 1985; Ebeling et al., 1985; Schiel and Foster, 1986). In addition to widespread declines in abundance of giant kelp from severe storms or strong El Niño events (Dayton, 1985; Tegner and Dayton, 1987), the dynamical behavior of local, even adjacent forests can differ (Dayton et al., 1984; Nisbet and Bence, 1989). Further, the density and sizes of kelp plants within established beds can change over time (Dayton et al., 1984). The occurrence and density of *Macrocystis* can in turn affect the abundance and composition of understory algae and invertebrates on a reef (Schiel and Foster, 1986; Kennelly, 1989).

The consequences of spatial variation in giant kelp on reef fishes are not well known. Giant kelp is thought to benefit many species of rocky inshore fish (Table 1), although some negative associations have also been observed. Differences in composition of fish assemblages on reefs with and without *Macrocystis* have been reported (Limbaugh, 1955; Quast, 1968; Ebeling et al., 1980a; 1980b; Larson and DeMartini, 1984; Stephens et al., 1984; Patton et al., 1985; Bodkin, 1986; Carr, 1989). Fewer studies have explored possible quantitative relationships between density of kelp and that of fish (Ambrose, 1987; DeMartini and Roberts, 1990). Further, mechanism(s) underlying observed patterns have rarely been addressed. Carr (1989) experimentally showed that the presence of giant kelp dramatically enhanced recruitment of some rocky inshore fishes, and suggested that effects on

recruitment could explain some of the observed spatial variation in composition of the fish assemblage. The influence of giant kelp on understory algae and invertebrates, upon which some reef fish depend, has also been implicated as a possible mechanism (Carr, 1989).

Here we report quantitative relationships between the presence and density of giant kelp and the local density of particular substrate-associated fish. Our intent is to establish the degree to which species of fish that share particular reproductive modes and resource requirements show similar associations with giant kelp. The results strongly suggest that the effect of giant kelp on reef fishes is predictable and dependent on the ontogenetic resource requirements of each species.

METHODS

Field work was conducted at two Channel Islands off the coast of southern California, USA [Santa Catalina Island (33°28'N: 118°30'W) and Santa Cruz Island (34°05'N: 119°40'W)]. Study areas were shallow subtidal (<15 m bottom depth) rocky reefs having canopy-forming giant kelp (*Macrocystis pyrifera*), foliose macroalgae up to 1 m tall (common forms included *Dictyopteris* sp., *Pachydictyon* sp., *Zonaria farlowii*, *Eisenia arborea*, *Colpomenia* sp., *Sargassum palmeri*, *Rhodomenia* sp., *Gelidium robustum*, *Laminaria farlowii* and *Calliarthron* sp.), and turf (a low-growing matrix of small plants, colonial animals and debris). Percent cover of understory substrates was estimated at each site using line transects (that followed depth contours) where densities of fish were estimated (see below). The substrate under randomly selected points was determined (N = 400 points per site). If present, giant kelp was quantified by counting individual plants (>1 m tall) in band transects used to quantify fish (see below); occasionally, kelp was estimated from the line transects used to estimate cover of benthic substrates.

We estimated the density of selected substrate-associated fishes that represented two different reproductive modes. These included four species of live-bearing Embiotocids that give birth to large, well-developed young [striped surfperch (*Embiotoca lateralis*), black surfperch (*Embiotoca jacksoni*), pile surfperch (*Damalichthys vacca*) and kelp surfperch (*Brachyistius frenatus*)] and three species having a planktonic larval stage [kelp bass (*Paralabrax clathratus*), giant kelpfish (*Heterostichus rostratus*), and kelp rockfish (*Sebastes atrovirens*)].

Counts of fish were made by divers using SCUBA on band transects (30·1·2 m for kelp bass and island kelpfish; 40·2·2 m for the others) along a depth contour. Two transects were counted: one on the bottom along a depth contour and a second in the water column beneath the surface canopy. All counts were made during daylight hours (0800–1600 h) under bright light conditions when water visibility exceeded 10 m. Fish were classified as young-of-year (Age 0) or older (Age 1+) based on estimated body size and/or morphological characteristics. Counts of young-of-year and older fish of a species were combined when the two age classes had extremely similar density relationships with giant kelp. The behavior of individual fish was not affected by divers with the exception of very large kelp bass (which were rare at our sites).

Two tests of the reliability of our estimation technique were performed. First, the degree to which our sampling technique underestimated density of such cryptic fish as the giant kelpfish, which is well camouflaged (in color and shape) with *Macrocystis* fronds was explored. Densities were estimated from two sets of eight replicate counts (bottom and canopy transects) within a kelp bed during August 1976. The first set of replicates was slow and methodical, with the observer attempting to locate concealed kelpfish by inspecting individual kelp fronds. These counts were compared to those made on the same day using the normal method. The two techniques did not yield significantly different density estimates (Coyer, 1979).

Second, the repeatability of density estimates was examined for four species (kelp bass, kelp rockfish, kelp surfperch, giant kelpfish) by counting fish daily over a consecutive seven-day period. On each day, counts of both the bottom and canopy transects were conducted in a single kelp forest. No significant day-to-day differences were found for any species, indicating that our standard estimation technique was highly repeatable (for details see Coyer, 1979). We thus are confident that any observed differences in density of fish among reefs were not due to sampling artifacts.

RESULTS

Direct Effects of Giant Kelp on Fish.—Both young-of-year and older stages of several species live in close association with giant kelp, and their densities on a reef were highly correlated with density of giant kelp. The strongest links occurred

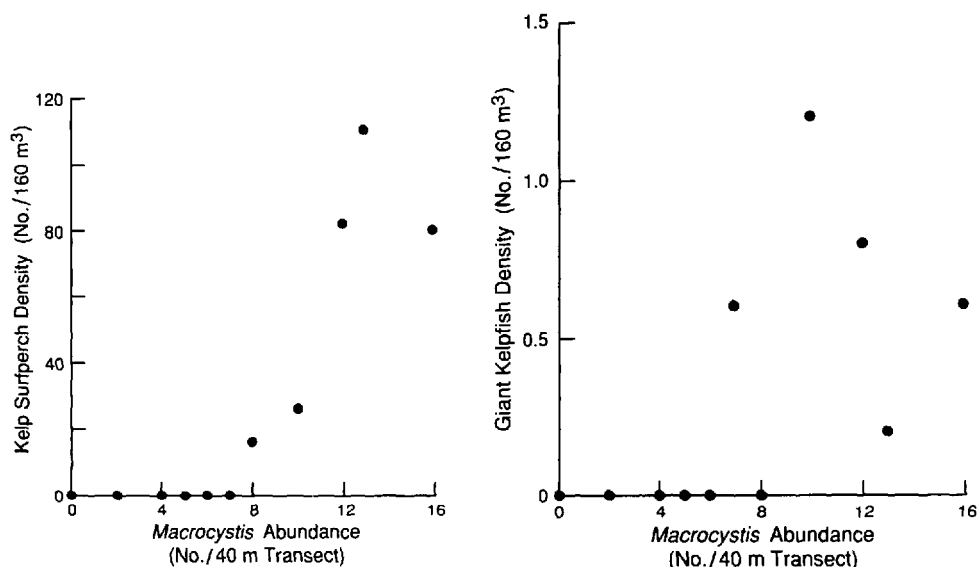


Figure 1 (left). The relationship between density of kelp surfperch, *Brachyistius frenatus* (ages combined), and density of giant kelp on 11 reefs on Santa Catalina Island ($r = 0.85$; $P < 0.01$). Figure 2 (right). The relationship between density of giant kelpfish, *Heterostichus rostratus* (ages combined), and density of giant kelp on 11 reefs on Santa Catalina Island ($r = 0.60$; $P < 0.04$).

for the kelp surfperch, *Brachyistius frenatus* (Fig. 1), and the giant kelpfish, *Heterostichus rostratus* (Fig. 2). Our data indicate that reefs with little or no giant kelp lacked young-of-year and older stages of these two species. Further, the data suggest that a threshold density of giant kelp (8 to 10 plants 40 m^{-1} line transect) was necessary before substantial densities of kelp surfperch and giant kelpfish occupied a kelp forest. The kelp rockfish, *Sebastes atrovirens* (Fig. 3) was also absent from reefs lacking *Macrocystis*, and likewise appeared to require a threshold amount of giant kelp before occupying a reef. However, no strong correlation was detected between density of giant kelp and density of kelp rockfish (Fig. 3).

Kelp bass, *Paralabrax clathratus*, typify fish in which only one life stage was closely associated with giant kelp. The abundance of young-of-year kelp bass (Fig. 4), but not older individuals (Fig. 5), was positively and strongly related to the amount of kelp present on a reef. Unlike other species, young-of-year kelp bass were present at very low densities of giant kelp, and there was no suggestion of a threshold.

Indirect Effects on Fish Mediated by Effects of Kelp on Understory Algae.—Giant kelp can alter the composition and density of understory algae on a reef. We found a strong negative relationship between the density of giant kelp on a reef and the abundance of foliose understory algae (Fig. 6). There was also an inverse correlation between cover of foliose understory algae and cover of turf ($r = -0.88$). At high densities of giant kelp, foliose algae was essentially replaced by turf.

Two fish species (black surfperch, *Embiotoca jacksoni*, and pile surfperch, *Damalichthys vacca*) derived a positive benefit from the effect of giant kelp on the understory. The densities of both age classes of black surfperch were positively and strongly correlated with cover of turf (Fig. 7). There was a significant but weaker trend for density of pile surfperch to be inversely correlated with cover of foliose algae (Fig. 8).

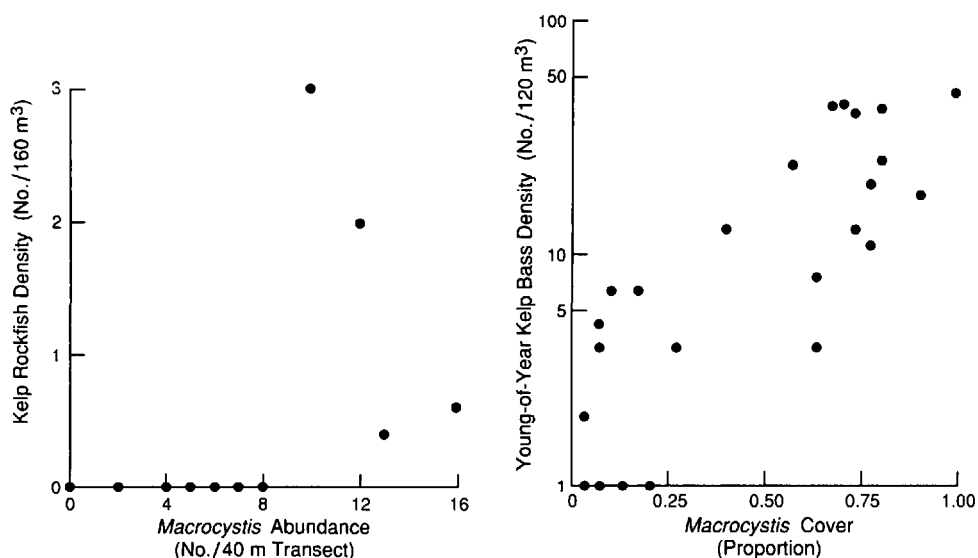


Figure 3 (left). The relationship between density of kelp rockfish, *Sebastes atrovirens* (ages combined), and density of giant kelp on 11 reefs on Santa Catalina Island ($r = 0.48$; NS).

Figure 4 (right). The relationship between density of young-of-year kelp bass, *Paralabrax clathratus*, and cover of giant kelp at 27 reefs at Santa Catalina Island ($r = 0.84$; $P < 0.001$). Data were log transformed for analysis.

The effect of giant kelp on understory algae had a negative effect on another species of surfperch, the striped surfperch (*Embiotoca lateralis*). The density of striped surfperch was positively correlated with density of foliose red algae (Fig. 9), which in turn was adversely affected by density of giant kelp.

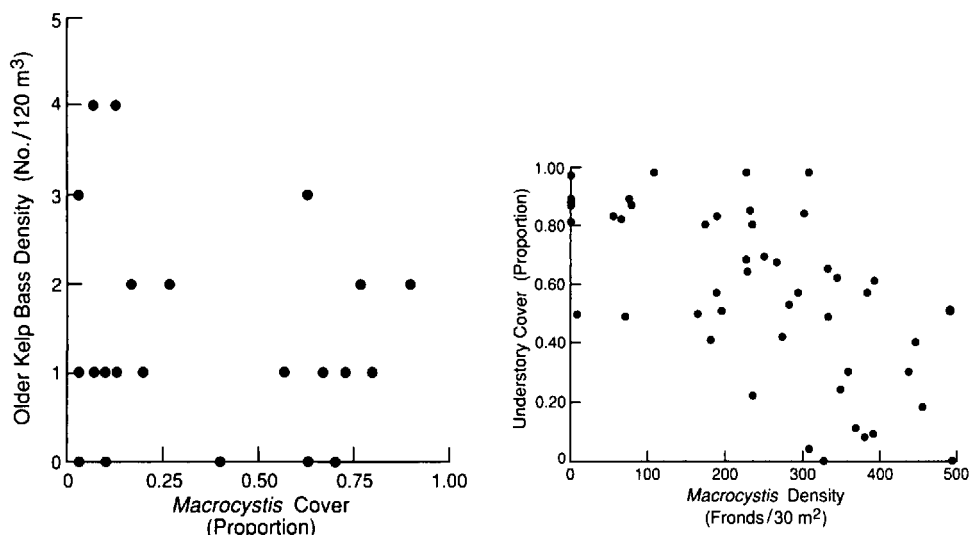


Figure 5 (left). The relationship between density of older kelp bass, *Paralabrax clathratus*, and cover of giant kelp at 25 reefs on Santa Catalina Island ($r = 0.05$; NS).

Figure 6 (right). Cover of understory foliose algae plotted against cover of giant kelp at 47 reefs on Santa Catalina Island ($r = -0.66$; $P < 0.001$; after Carr, 1989).

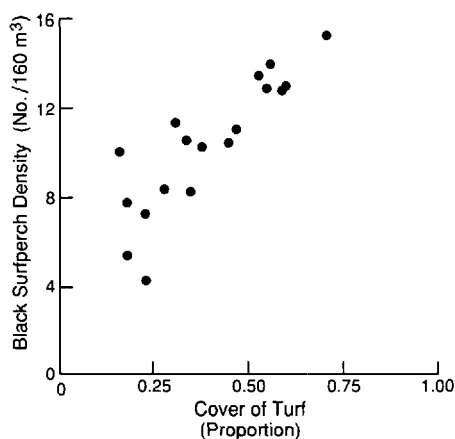


Figure 7 (left). The relationship between density of black surfperch, *Embiotoca jacksoni* (ages combined), and cover of turf at 18 reefs on Santa Cruz Island ($r = 0.86$; $P < 0.001$). There was a significant inverse correlation in density of turf and density of foliose algae ($r = -0.88$; 24 df; $P < 0.001$) at Santa Cruz Island.

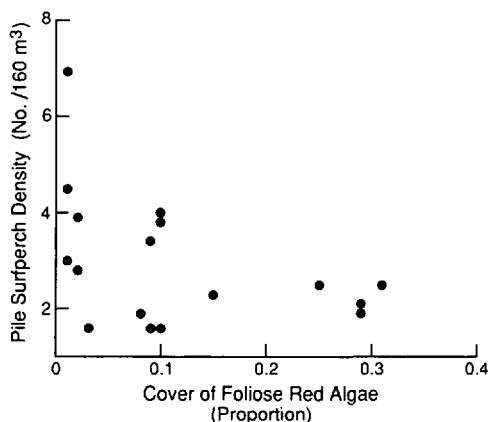


Figure 8 (right). The relationship between density of pile surfperch, *Damalichthys vacca* (ages combined), and cover of foliose red algae at 18 reefs on Santa Cruz Island ($r = -0.44$; $P < 0.05$; see Fig. 7 caption).

DISCUSSION

The results presented here indicate that the presence and density of giant kelp on a reef in the southern California bight were good predictors of the presence and local density of the reef fishes we examined. The relationship between giant kelp and one or more life stages of reef fish can be either positive or negative. As discussed below, the particular form of the relationship appears to reflect ontogenetic resource requirements of that fish (Table 1). Further, our results indicate that strong spatial relationships with giant kelp exist independent of the particular mode of recruitment (planktonic or livebearing) by reef fishes.

Spatial patterns notwithstanding, mode of recruitment no doubt plays a significant role in a dynamical context. For example, the experiments of Carr (1989) show that, for species having planktonic larvae, adults need not be present in a particular kelp forest for their young to recruit there, in marked contrast with live-bearing surfperch (Coyer, 1979). The availability of appropriate settlement or nursery areas, such as provided by giant kelp, can have a substantial effect on the occurrence and strength of larval recruitment to a local reef (Jones, 1984; Shulman, 1984; Behrents, 1987; Carr, 1989). Thus, temporal variability in giant kelp on a reef, a common phenomenon in southern California (Coyer, 1979; Dayton, 1985; Ebeling et al., 1985; Schiel and Foster, 1986), can result in temporal fluctuation in the number of larval recruits. This source of variability is in addition to vagaries associated with the planktonic larval phase (Cowen, 1985; Victor, 1986; Doherty and Williams, 1988).

The potential effect of variation in giant kelp on population dynamics of a reef fish, together with the influence of ontogenetic resource requirements, is cogently illustrated by the kelp bass (*Paralabrax clathratus*). Kelp bass only have one life stage with a positive affinity for giant kelp; larvae are planktonically dispersed and accumulate among giant kelp plants during settlement (Larson and DeMartini, 1984; Carr, 1989) where young feed on invertebrates (Coyer, 1979). We found

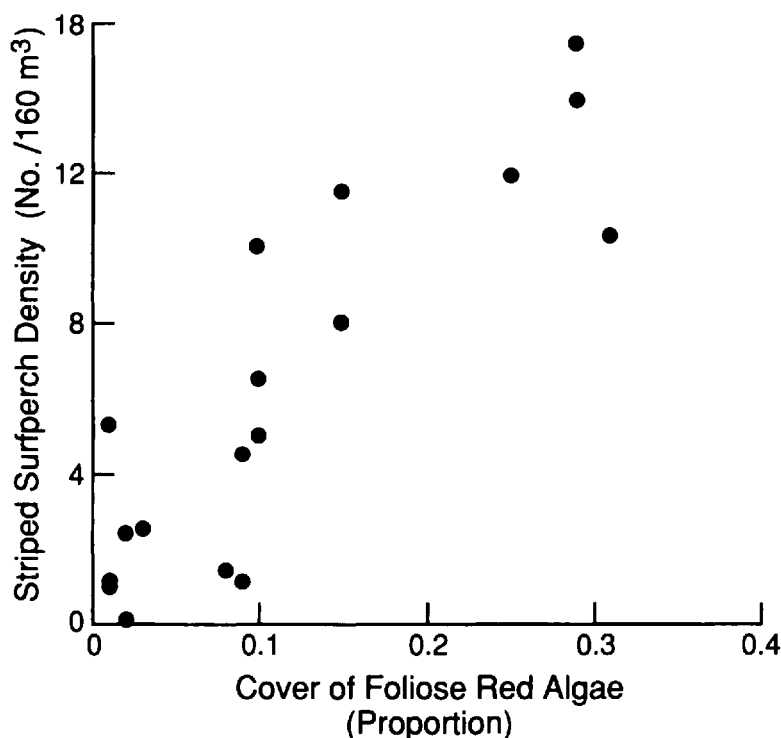


Figure 9. The relationship between density of striped surfperch, *Embiotoca lateralis* (ages combined), and cover of foliose red algae at 18 reefs on Santa Cruz Island ($r = 0.87$; $P < 0.001$; see Fig. 7 caption).

Table 1. Summary of effects giant kelp has on local density of reef fishes we examined (species are grouped into mode of reproduction; older stages include ages ≥ 1 ; + = positive, - = negative, and 0 = no effect of kelp)

Species	Life stage	Effect	Mechanism
Species with planktonic stage			
<i>Paralabrax clathratus</i>	young-of-year	+	provides nursery, refuge
	older stages	0	
<i>Sebastes atrovirens</i>	young-of-year	+	provides nursery, refuge
	older stages	+	provides foraging habitat
<i>Heterostichus rostratus</i>	young-of-year	+	provides nursery, refuge
	older stages	+	provides foraging habitat
<i>Gibbonsia elegans</i>	young-of-year	-	shading reduces nursery & removes refuge
	older stages	-	shading reduces foraging habitat & refuge
Live-bearing species			
<i>Brachyistius frenatus</i>	young-of-year	+	provides nursery, refuge; more local breeding adults
	older stages	+	provides refuge, foraging habitat
<i>Damalichthys vacca</i>	young-of-year	+	more local breeding adults
	older stages	+	shading increases foraging space
<i>Embiotoca jacksoni</i>	young-of-year	+	more local breeding adults
	older stages	+	shading increases foraging space
<i>Embiotoca lateralis</i>	young-of-year	-	fewer local breeding adults
	older stages	-	shading reduces foraging space

Table 2. A partial list of reef fishes thought to be influenced by the presence of giant kelp, *Macrocystis pyrifera*

Fish species	Effect of giant kelp	Source
<i>Brachyistius frenatus</i> (Kelp Surfperch)	+	Coyer, 1979; Ambrose, 1987; DeMartini and Roberts, 1990
<i>Damalichthys vacca</i> (Pile Surfperch)	+	DeMartini and Roberts, 1990
<i>Embiotoca jacksoni</i> (Black Surfperch)	+	Schmitt and Holbrook, unpubl.; DeMartini and Roberts, 1990
<i>Heterostichus rostratus</i> (Giant Kelpfish)	+	Carr, 1989; DeMartini and Roberts, 1990
<i>Paralabrax clathratus</i> (Kelp Bass)	+	Coyer, 1979; Carr, 1989; Larson and DeMartini, 1984; DeMartini and Roberts, 1990
<i>Sebastes atrovirens</i> (Kelp Rockfish)	+	Coyer, 1979; Carr, 1983
<i>Sebastes carnatus</i> (Gopher Rockfish)	+	Carr, 1983
<i>Sebastes caurinus</i> (Copper Rockfish)	+	Burge and Schultz, 1973; Miller and Geibel, 1973; Carr, 1983
<i>Sebastes melanops</i> (Black Rockfish)	+	Leaman, 1976; Carr, 1983
<i>Sebastes paucispinis</i> (Bocaccio)	+	Moser, 1967; Carr, 1983
<i>Sebastes serranoides</i> (Olive Rockfish)	+	Miller and Geibel, 1973; Carr, 1983
<i>Alloclinus holderi</i> (Island Kelpfish)	-	Carr, 1989
<i>Embiotoca lateralis</i> (Striped Surfperch)	-	Schmitt and Holbrook, unpubl.
<i>Gibbonsia elegans</i> (Spotted Kelpfish)	-	Carr, 1989
<i>Paralabrax nebulifer</i> (Barred Sandbass)	-	Ambrose, 1987

that density of young-of-year, but not older, kelp bass was strongly related to density of giant kelp among reefs. Kelp bass become piscivorous as they age, and older kelp bass range over a variety of habitats in search of invertebrate and fish prey (Collyer and Young, 1953; Quast, 1968; Feder et al., 1974; Coyer, 1979). We found that older kelp bass, but not young-of-year, were common on reefs devoid of giant kelp. Because kelp bass are long-lived, their abundance can vary relatively little from year to year despite large changes in local occurrence of giant kelp (Stephens et al., 1984; Ebeling and Laur, 1988). However, our data suggest that prolonged regional absence of giant kelp would represent a recruitment bottleneck that could ultimately result in a (lagged) reduction in adult density. The pattern for kelp bass appears representative of many rockfish (Table 2), a group of species that have planktonic larvae and depend on giant kelp only as a nursery for young (Moser, 1967; Leaman, 1976; Burge and Schultz, 1973; Miller and Geibel, 1973; Carr, 1983). All of these species are long-lived, generalized predators that, as adults, consume invertebrates and small fishes from a variety of benthic habitats (Hallacher and Roberts, 1985).

As expected, the effect of *Macrocystis* on local fish density was stronger for species that have high affinity for giant kelp during several ontogenetic stages. For example, both young and older life stages of the kelp surfperch (*Brachyistius frenatus*), a live-bearing species, depend on giant kelp for refuge from predators and for crustacean food (Quast, 1968; Hobson, 1971; Bray and Ebeling, 1975; Coyer, 1979). We found a strong positive relationship between density of giant kelp and local density of kelp surfperch. A similar but less strong relationship was detected for the giant kelpfish (*Heterostichus rostratus*). Giant kelpfish, which has a planktonic larval stage, recruits in greater numbers when giant kelp is present on a reef (Carr, 1989). Following settlement, young and older *H. rostratus* are highly secretive, sit-and-wait predators of mobile crustaceans (primarily shrimp) associated with kelp and other similar macroalgae (Coyer, 1979). Unlike kelp

surfperch, some adult giant kelpfish disassociate with giant kelp, especially males who establish nests in understory algae (Coyer, 1982; Stepien, 1986).

Although both young-of-year and older kelp rockfish (*Sebastes atrovirens*) depend on resources provided by giant kelp (Quast, 1968; Bray and Ebeling, 1975; Coyer, 1979), we failed to detect a significant positive correlation between this fish and kelp densities. There was, however, a strong effect of giant kelp on the local occurrence (presence-absence) of kelp rockfish, which was absent on reefs that lacked giant kelp. Young-of-year kelp rockfish, which recruit from the plankton, have similar food and shelter requirements to kelp surfperch (Coyer, 1979; Singer, 1985). Older *S. atrovirens* feed on both invertebrates and small fishes they ambush a short distance from kelp fronds (Hobson and Chess, 1976; Coyer, 1979; Hallacher and Roberts, 1985).

It appears that a minimum density of giant kelp might be necessary before populations of kelp surfperch (*B. frenatus*), giant kelpfish (*H. rostratus*), or kelp rockfish (*S. atrovirens*) occur on a reef. The reasons for such a "threshold" remain unclear, although a low density of kelp might provide too few resources to sustain a population, or might be new relative to the colonization rate of the fishes.

In general, giant kelp had direct, positive effects on life stages of reef fish that used kelp for feeding and/or shelter from predators. Our data also show that positive effects need not be direct, as in the cases described above. Because shading by giant kelp can reduce understory foliose algae and enhance the cover of turf (Schiel and Foster, 1986; Carr, 1989; Kennelly, 1989; this paper), giant kelp can indirectly affect species that use understory habitat. Black surfperch (*Embiotoca jacksoni*) and pile surfperch (*Damalichthys vacca*), which require turf or areas devoid of understory macroalgae to harvest invertebrate prey (Laur and Ebeling, 1983; Holbrook and Schmitt, 1984; Schmitt and Holbrook, 1984; Stouder, 1987), have larger populations in areas with greater density of kelp (DeMartini and Roberts, 1990; Ambrose, 1987; this paper).

The indirect effects of giant kelp also can be negative. For example, striped surfperch require foliose understory algae as foraging microhabitat, and visually pick amphipods and isopods from algal surfaces (Schmitt and Coyer, 1982; 1983; Schmitt and Holbrook, 1984; Laur and Ebeling, 1983). The density of striped surfperch (*Embiotoca lateralis*) was positively related to the amount of foliose algae present on a reef, and densities are lower where giant kelp reduces understory algae (this paper; Holbrook and Schmitt, unpubl.). Thus, two members of the genus *Embiotoca* (black surfperch and striped surfperch) show opposite relationships with giant kelp, which can be explained by the differences in their modes of foraging. Striped surfperch only feed effectively from foliose algae (which is reduced by giant kelp), whereas black surfperch can effectively exploit turf (which is enhanced by giant kelp).

We expect that other reef fishes that require foliose understory algae will be adversely affected by the shading effect of giant kelp. For example, the spotted kelpfish (*Gibbonsia elegans*) requires foliose understory algae throughout its benthic life. Planktonic larvae recruit to understory algae, where older individuals remain to hide from predators and feed on small invertebrates (Stepien, 1986). Carr (1989) found that populations of this species were adversely affected by giant kelp, again through the reduction of understory algae. We suspect, however, giant kelp will affect the occurrence (presence-absence) of such species as striped surfperch and *Gibbonsia* only when the forest is so dense that all appropriate understory algae are eliminated.

Although giant kelp provides a major source of algal structure on reefs in southern California, studies addressing its role in determining the composition

of reef fish assemblages have led to mixed conclusions. Several workers (Ebeling et al., 1980a; 1980b; Larson and DeMartini, 1984; Ambrose, 1987; Ebeling and Laur, 1988) have argued that giant kelp modifies the assemblage of fish on a reef, but others (Stephens et al., 1984; Patton et al., 1985) have concluded that giant kelp has little influence on species composition. The present work suggests that the nature of a kelp forest—its presence, density, and influence on understory algal—contributes to its effect on the species composition and local density of the fish assemblage. We found qualitatively different relationships between density of giant kelp and standing stock of particular species of fish, although the causal mechanisms remain incompletely understood. The relationship can be positive or negative, arise from direct or indirect effects, and influence some or all life stages. Nevertheless, reef fishes with similar ontogenetic resource requirements appear to share a common relationship with the presence and density of giant kelp.

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