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**Patterns, Mechanisms, and Consequences of Recruitment
of a Temperate Marine Reef Fish**

by
Mark H. Carr

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UNIVERSITY OF CALIFORNIA
Santa Barbara

Patterns, Mechanisms, and Consequences of Recruitment
of a Temperate Marine Reef Fish

A dissertation submitted in partial satisfaction of the
requirements for the degree of

Doctor of Philosophy

in Biology

by

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June 1991

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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.

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ABSTRACT

Patterns, Mechanisms, and Consequences of Recruitment of a Temperate Marine Reef Fish

by

Mark Harrison Carr

Patterns of spatial and temporal variation in recruitment of larval kelp bass, *Paralabrax clathratus*, to reefs at Santa Catalina Island, CA., are described. Much of this variation was explained by changes in time and space in the density of the surface-canopy forming giant kelp, *Macrocystis pyrifera*. Density manipulations of giant kelp revealed a causal effect on recruitment of kelp bass, although the positive relationship between densities of kelp bass recruits and *Macrocystis* was asymptotic. The asymptote resulted from density-dependent effects of *Macrocystis* on the morphology (structural complexity) of individual plants; recruitment of kelp bass was a linear function of structural complexity of giant kelp. These results indicate that features of the settlement habitat, and not a limited supply of larvae, contributed most to variation in local recruitment of kelp bass.

I explored alternate hypotheses regarding mechanisms underlying the relationship between *Macrocystis* and recruitment of kelp bass. The evidence indicates that larval kelp bass settle on *Macrocystis* primarily because this alga is the only structure encountered by larvae, which are distributed throughout the

water column. Variation in larval supply could not explain differences in recruitment between reefs with and without *Macrocystis*. Choice experiments revealed that newly settled kelp bass displayed no preference for *Macrocystis* over other common algae. Greater recruitment to *Macrocystis* than other algal habitats was not explained by differences in availability of food or in post-settlement growth of recruits. While settlement to *Macrocystis* was best explained by passive encounter rather than active choice by kelp bass larvae, subsequent movement from the site of settlement was inhibited by risk of predation and the presence of sufficient food.

Predation, primarily by older (≥ 1 yr) kelp bass, influenced the distribution and density of recruits. Of the factors examined, risk of predation was influenced mostly by size of the recruit and local abundance of predators. Predators were consistently most common near the bottom, regardless of the presence or absence of *Macrocystis*. Consequently, the upper portion of *Macrocystis* forests is a spatial refuge for recently settled kelp bass.

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CHAPTER 1

EFFECTS OF MACROALGAL DYNAMICS ON PATTERNS OF TEMPERATE REEF FISH RECRUITMENT

INTRODUCTION

Plant and animal populations may often be comprised of many separate local populations whose members interact and breed with one another but are isolated from members of other local populations. Such local populations may be loosely linked by the dispersal of offspring. Often, nearly all offspring disperse away from local parental populations, effectively decoupling local larval production and the supply of potential recruits to that population. Therefore, recruitment to a local population may depend on the supply of offspring produced elsewhere. Such open populations (*sensu* Caswell 1978) are often characteristic of sessile organisms with highly dispersive propagules: for example, many terrestrial plants with wind-borne, ingested and adhesive seeds (for reviews see van der Pijl 1972, Howe and Smallwood 1982, Fenner 1985, Murray 1986, and Sorensen 1986); marine macroalgae with planktonic spores (Reed et. al. 1988); and marine invertebrates with planktonically dispersed eggs or larvae (Thorson 1950, 1966, Yoshioka 1982, Underwood and Denley 1984, Connell 1985, Roughgarden et. al. 1985, 1988, Underwood and Fairweather 1989, Hughes 1990, Raimondi 1990). Open populations are also characteristic of many mobile species in heterogeneous habitats, particularly those with a highly dispersive stage but otherwise limited movement: for example, many terrestrial insects (Southwood 1962, Johnson 1969, Dingle 1972, Karieva 1986); spiders (Duffey 1956, Richter 1970); and marine reef fishes (Ehrlich 1975, Sale 1980, Williams 1980, Doherty 1983, Victor 1983, 1986, Doherty and Williams 1988, Mapstone and Fowler 1988, Warner and Hughes 1989). The determination of the relative contribution of various factors (e.g., propagule

supply, settlement cues, predation, competition, etc.) to each phase of the recruitment process (i.e., production, dispersal, settlement, and post-settlement) is critical to our understanding of the interactions among local open populations (Roughgarden et. al. 1985, Roughgarden and Iwasa 1986).

Marine reef fishes exemplify populations composed of many local open populations, each associated with a particular coral or rocky reef. Substrate-associated juveniles and adults often exhibit limited movement among reefs whereas their pelagic larvae can be widely dispersed by currents. Larval replenishment has been demonstrated to have strong effects on the size and demography of local reef fish populations (e.g., Williams 1980, Victor 1983, 1986, Doherty 1983, Jones 1987, 1990, Warner and Hughes 1989, Forrester 1990) as well as the species composition (i.e., relative abundance) of reef fish assemblages (e.g., Ehrlich 1975, Sale 1980, Sale and Douglas 1984, Doherty and Williams 1988). From these studies, the availability of larvae has often been argued to be the most important determinant of recruitment to a local population (see review by Doherty and Williams 1988). However, almost all of these studies have been restricted to coral reef fishes, with only a few examples from temperate rocky reef systems.

One important way in which coral and temperate rocky reefs differ from one another is in the extent to which macroalgae can contribute to their physical structure. Although macroalgae can be abundant on some coral reefs, the larger species (e.g. kelps) characteristic of many temperate reefs are absent. Perhaps because of this, studies of coral reef fish recruitment have not addressed the potential importance of macroalgae on the distribution and dynamics of larval recruitment. In contrast, macroalgae often constitute the

majority of physical structure of temperate rocky reefs and their abundance is often highly dynamic within and among reefs (Dayton et al. 1984, Dayton 1985, Ebeling and Laur 1988, Schiel and Foster 1986, Reed et al. 1988, Nisbet and Bence 1989). Consequently, temporal variation of habitat structure may have a stronger affect on the distribution and abundance of recruits than is currently suggested by studies from coral reefs. However, effects of the variability of macroalgae on the spatial and temporal variation in recruitment of temperate reef fishes have been largely unexplored.

The kelp bass, *Paralabrax clathratus*, is a temperate reef fish with pelagic eggs and larvae dispersed by currents for approximately 3 to 4 weeks (Carr unpublished data). Whereas larvae may disperse great distances, juveniles and adults probably move much less (< 0.16 km, Young 1963). The giant kelp, *Macrocystis pyrifera*, is the dominant macroalga on rocky reefs throughout the range of the kelp bass. Previous studies have indicated that this macroalga provides an important substrate for local kelp bass recruitment (Larson and DeMartini 1984, Carr 1989). Consequently, patterns of kelp bass replenishment may be influenced by the spatial distribution and temporal dynamics of *Macrocystis* forests.

Here, I describe the patterns of larval recruitment of kelp bass and the effects of *Macrocystis* dynamics on the spatial and temporal variability of recruitment among reef-associated populations. I examine the functional relationship between the density of *Macrocystis* and kelp bass recruits in order to determine the mechanisms producing this relationship. Because individual plant architecture and biomass vary as a function of plant density, I emphasize

the importance of the density dependent growth form of *Macrocystis* as it may affect kelp bass recruitment.

METHODS

All observations and experiments were conducted along the northwest coast of Santa Catalina Island ($33^{\circ}27'N$: $118^{\circ}29'W$), 40 km offshore of southern California. Its rocky reefs, separated from one another by sand embayments, discontinuities in the coastline, or deep (> 30 m) water, differ from one another in abundance and composition of algae and vertical relief of the rocky substratum. Dominant algae include the surface canopy-forming giant kelp, *Macrocystis pyrifera* (hereafter *Macrocystis*), and several understory species, including *Sargassum palmeri*, *Dictyopteris* spp., *Eisenia arborea*, and *Zonaria farlowi*. Generally, cover of understory algae is reduced beneath the surface canopy of *Macrocystis* (Reed and Foster 1984, Schiel and Foster 1986, Carr 1989). *Macrocystis* forests exhibit strong spatial and temporal variation at Santa Catalina as elsewhere throughout its range (see references in Introduction).

After larval kelp bass (8-11 mm standard length, SL) disperse in the plankton for approximately 3 weeks, they settle as post-larvae on shallow reefs (depth \leq 10 m) from mid-July through September (Carr unpublished data). Tagging studies suggest adults move little (usually < 0.16 km, Young 1963). Consequently, the planktonic dispersal of larvae may be the only link among local populations that are spatially isolated.

I. Influence of local habitat on kelp bass recruitment.

Kelp bass recruitment, defined here as the number of 30-70 mm total length (TL) individuals observed at the end of the three month (July-September) settlement period, was sampled from 10 to 12 reefs at Santa Catalina from 1985 to 1989. Habitat characteristics and kelp bass recruitment were recorded in 60 m³ transects during Fall. Each 60 m³ transect consisted of two 1 X 1 X 30 m segments; one at mid-depth above the reef and the other along the bottom beneath the first transect. Kelp bass were classified by size (30-70, 70-150, 150-200, 200-250, and >250 mm TL) corresponding to <1, 1-2, 2-3, 3-4 and >4 yr age classes (see Young 1963 and Coyer 1979 for age-length relationship).

On each reef, transects were conducted at three bottom depths (3, 7 and 10 m). Habitat variables recorded along each transect included: bottom depth, percent cover of rock and sand, rock relief (classified as 0, 0-1, > 1 m relief), percent cover of understory algae, and density, size (number of stipes) and percent cover of *Macrocystis* canopy. I used a stratified random-point contact method to assess percent cover; the substratum type, algal species, and presence of *Macrocystis* canopy were recorded at two randomly located points per meter along the bottom transect (60 points total per transect). The number of stipes (≥ 1 m high) per *Macrocystis* plant within a 1 m wide swath along the transect was counted to determine the total density of stipes and plants (number per 30 m²) and mean plant size (stipes per plant).

Stepwise multiple regression was used to determine the combination of independent habitat variables which best explained among-transect variation in

the density of kelp bass recruits. Selection of the best model was based on the forward stepwise procedure (SAS) for each of the five years in which recruitment was measured.

II. Relationship between spatial and temporal variation of kelp bass recruitment and *Macrocystis* abundance.

If local kelp bass recruitment is an increasing function of *Macrocystis* abundance, then the greater the fluctuation in *Macrocystis*, the greater the fluctuation in kelp bass recruitment, both among reefs and among years. To determine if the spatial (among reef) variabilities of kelp bass recruitment and *Macrocystis* abundance were related, I used a linear regression to test for a positive relationship between the coefficients of variation (CV) of these two variables among the five sampling years. The relationship between temporal (among year) variabilities of these two variables was tested in the same manner among eight reefs. Two of the ten sampled reefs were excluded because they lacked *Macrocystis* during the five year sampling period. Annual recruitment and *Macrocystis* density for each reef were defined as the mean number of kelp bass recruits and *Macrocystis* stipes, respectively, counted on visual transects as described above in Section I.

III. Relationship between recruitment and 1 year old kelp bass density.

To determine if patterns of kelp bass recruitment are reflected in the subsequent abundance of older juveniles, I tested for a significant relationship

between the density of kelp bass recruits on a reef and the density of 1 year old individuals on that reef the following year. Recruitment to a reef was assumed to be independent among years (i.e., a new cohort of recruits settled from out of the plankton each year). The densities of recruits and subsequent 1 year olds were compared on each of eight reefs between years over a period of four years (1985-1988), providing 32 independent comparisons. I also tested for a significant relationship between estimates of the density of recruits and of subsequent 1 year olds, combined across reefs, over the same four years.

IV. Experimental test of the influence of *Macrocystis* density on kelp bass recruitment

To test the hypothesis that a greater local density of *Macrocystis* plants produces a greater local density of kelp bass recruits, I manipulated the plants in 500 m² (20 x 25 m) plots to three density levels (N = 3 plots each): "high" (above-average plant density in plots prior to manipulation), "medium", and "low" (by removing whole plants from the substratum or severing plants at the basal dichotomy just above the holdfast in other randomly chosen plots). Plant density in the high density plots was estimated from 5 randomly located 2 X 15 m belt transects per plot; plant densities in the medium and low density levels were reduced to approximately 50 and 20 percent of the high density levels, respectively. Each of the three density levels was randomly allocated to one of three blocks, all within 0.5 km of one another, (i.e., randomized block design). Since block effects were not significant (with a non-replicated analysis of variance; P ranged from 0.22 to 0.83), I considered blocks as replicates.

Macrocystis plants often grow very close to one another, the vertically growing stipes of several different individuals becoming closely intermingled. Therefore, I defined a *Macrocystis* "plant" as an aggregation of approximately 20 stipes (sometimes incorporating stipes of several individuals), which was the average number per plant in the study area. Mean plant size (number of stipes) was estimated from the same randomly selected plants sampled for kelp bass recruitment ($n = 8$ and 12 plants per plot in 1986 and 1987, respectively). All density manipulations were completed by mid-July, prior to settlement of kelp bass.

Kelp bass recruitment among the nine plots was sampled over 5 consecutive days in October 1986 and 4 days in late September 1987. Randomly selected plants ($n = 8$ and 12 plants per plot in 1986 and 1987, respectively) were censused from top to bottom; in addition, 30 m^3 (1×2 wide $\times 15$ m) belt transects (1986 $n = 5$ per plot, 1987 $n = 8$ per plot) were sampled along the reef surface for kelp bass recruits (30-80 mm SL). Few recruits were encountered along bottom transects and their density did not differ significantly among *Macrocystis* density levels (see Results, Table 3). Therefore, the density (fish per 10 m^2) of kelp bass recruits was calculated for each plot as the product of the mean number of recruits per *Macrocystis* plant and the plant density of a plot. Plot means ($n = 3$) calculated from transects were compared among years and *Macrocystis* density levels with a two factor analysis of variance.

To determine whether differences in recruit density among *Macrocystis* density levels persisted, I sampled the density of recruits on 30 m^3 transects in June (8 months post-recruitment) of 1987 and 1988. Each 30 m^3 transect ($n = 8$ per plot) consisted of a $1 \times 1 \times 15$ m segment at mid-depth above the reef and

another along the reef surface. Plot means ($n=3$) calculated from transects were compared among years and *Macrocystis* density levels with a two factor analysis of variance.

Because individual plant morphology is often influenced by plant density (Harper 1977), I compared the structural complexity (number and biomass of *Macrocystis* blades per unit length of stipe) of *Macrocystis* plants growing at the different density levels. To measure complexity, I removed all blades from a 1 m section (at mid-depth) of each of four randomly selected plants per plot, recorded the number of stipes per plant, and damp weighed the blade material (including pneumatocyst). Total blade weight (and blade number) was divided by the number of stipes per plant. Mean blade weight (and number) per stipe was calculated from the four plants of each plot and compared (after log transformation) among density levels and blocks in a two factor, unreplicated ANOVA. Because plant size (mean stipes per plant) did not differ significantly among the experimentally manipulated density levels, and because kelp bass recruits use single plants as cover from predators rather than moving among several plants, blade biomass per plant provided a reasonable estimate of cover available for kelp bass recruits in each of the three *Macrocystis* densities.

I also monitored the density of older (≥ 1 yr) kelp bass in each *Macrocystis* density plot because older kelp bass are the most abundant potential predators of kelp bass recruits at Santa Catalina Island (Carr 1991a). Density of older kelp bass was estimated at four times during the experiment (October 1986 and 1987 and June 1987 and 1988) from 30 m^3 belt transects (consisting of a $1 \times 1 \times 15\text{ m}$ swath each at mid-depth and the bottom). Mean kelp bass density for each plot was calculated from 5 and 8 transects in June and

October, respectively. The density of older kelp bass was compared among *Macrocystis* densities using plot means as replicates ($n=3$) in a two factor (time by *Macrocystis* density) analysis of variance.

RESULTS

I. Influence of local habitat on kelp bass recruitment.

As measured by an independent variable's relative contribution (i.e., partial r^2) and its frequency of occurrence in each of the five annual multiple regression models, bottom depth and measures of *Macrocystis* abundance (mean plant size, total stipes per transect or canopy cover) explained the most variation in local kelp bass recruitment. Unlike other variables, depth and *Macrocystis* abundance were included in models for most of the five years examined (Table 1a). Although the strength of recruitment varied between years, recruitment was greater on transects in deeper water. This pattern was generally consistent among years (Figure 1, two factor ANOVA: year effect, $df = 4, F = 9.79, P = 0.0001$; depth effect, $df = 2, F = 19.94, P = 0.0001$; depth by year interaction, $df = 8, F = 1.72, P = 0.09$). The three measures of *Macrocystis* -- mean plant size, total stipes per transect, and percent cover -- were highly intercorrelated and much less correlated with depth (Table 2). Multiple regression models including only the deeper (bottom depth ≥ 7 m) transects, where the majority of recruits occurred, usually increased the variance explained by the regression models and again indicated a strong relationship

between *Macrocystis* abundance and kelp bass recruitment (Table 1b).

The strength of this relationship and the variance explained by the multiple regression models generally declined from 1985 to 1989 (Table 1 a,b). From 1985 to 1989, mean density of *Macrocystis* (stipes per transect) increased significantly (Figure 2; single factor ANOVA, $df = 4$, $F = 24.67$, $P = 0.0001$). During this period (1985 to 1989), there was also a significant relationship between kelp bass recruitment and *Macrocystis* density (Figure 2). However, as the mean density of *Macrocystis* increased among transects each year, the spatial variation (CV) in both *Macrocystis* density and recruit density declined (Figure 3). Significant negative relationships existed among years between mean *Macrocystis* density and among-transect CVs of *Macrocystis* density, and between mean *Macrocystis* density and among-transect CVs of kelp bass recruit density. Consequently, during years when *Macrocystis* was more abundant, *Macrocystis* explained less variation in recruitment of kelp bass, which was less variable; thus, the relationship between *Macrocystis* and patterns of kelp bass recruitment became less apparent.

II. Relationship between spatial and temporal variation of kelp bass recruitment and *Macrocystis* abundance.

The relationship between local *Macrocystis* abundance and kelp bass recruitment is manifested in spatial (within years, among reefs) and temporal (within reefs, among years) patterns of recruitment to reef associated populations. The coefficient of variation (CV) in kelp bass recruitment among reefs is positively related to the CV in *Macrocystis* density among reefs (Figure

4). Hence, kelp bass recruitment varies more among reefs during years in which *Macrocystis* density varies markedly as well. Also, annual differences in the CV of kelp bass recruitment between reefs are positively related to differences in CV of *Macrocystis* density (Figure 5). Therefore, reefs showing greater annual variation in *Macrocystis* density also exhibit greater annual variation in kelp bass recruitment.

The mean density of kelp bass recruits (per reef) was significantly related to *Macrocystis* density among reefs and years over the five year period of sampling (Figure 6). A nonlinear (asymptotic) regression model explained more variation in recruitment among reefs and years ($r^2 = 0.651$, $df = 39$, $P < 0.0001$) than a linear model ($r^2 = 0.493$, $df = 40$, $P = 0.0001$). The *Macrocystis* density corresponding to asymptotic recruit density (95% of total) was 130 stipes per 30 m^2 .

III. Relationship between densities of recruitment and 1 year old kelp bass.

Patterns of kelp bass recruitment appear to influence subsequent patterns of older (1 year) juvenile abundance among reefs and among years. The density of recruits on a reef was related positively to the density of 1 year old individuals in the following year (Figure 7). The mean density of juveniles in a year, averaged over all reefs, was also positively related to the mean density of recruits in the previous year (Figure 8).

IV. Experimental test of the influence of *Macrocystis* density on kelp bass recruitment.

Almost all individuals recruited to *Macrocystis* plants on the reefs where plant densities were manipulated. Where *Macrocystis* was absent, few fish were encountered near the bottom and there was no detectable difference in recruit density either among years or kelp density levels in open areas (Table 3). Using counts from *Macrocystis* plants, recruit densities (individuals per 10 m² of reef surface) among *Macrocystis* density levels showed no significant year effect ($df = 1, F = 0.36, P = 0.56$) nor year by *Macrocystis* density interaction ($df = 2, F = 0.73, P = 0.50$), thus indicating no detectable annual effect of *Macrocystis* density on kelp bass recruitment. Therefore, I pooled data among years for each *Macrocystis* density level. Density of kelp bass recruits was significantly lower at the lowest *Macrocystis* density but did not differ between the medium and high density levels (Figure 9; $df = 2, F = 11.0, P = 0.002$, REGWF means comparison). *Macrocystis* density is presented as stipe density, rather than plant density, to facilitate comparison between experimental results and reef surveys (Section II).

The pattern of kelp bass recruitment among *Macrocystis* densities persisted through the 8 months following recruitment. Like recruit density, the density of 8-month old kelp bass was significantly lower at the lowest *Macrocystis* density, but did not differ between the medium and high density levels (Table 4, $df = 2, F = 6.07, P = 0.017$, REGWF means comparison). Neither year main effect ($df = 1, F = 3.12, P = 0.11$) nor year by *Macrocystis* density interaction ($df = 2, F = 1.28, P = 0.316$) were significant, indicating no

detectable difference in the effect of *Macrocystis* on interannual recruitment.

The relationship between *Macrocystis* density and density of kelp bass recruits was non-linear (Figure 10). Beyond some intermediate plant density, further increases in *Macrocystis* density did not produce significant increases in kelp bass recruits. A non-linear, asymptotic regression model explained more variation in recruitment among plots ($r^2 = 0.345$, $df = 16$, $P = 0.01$) than a linear model ($r^2 = 0.262$, $df = 17$, $P = 0.03$). Therefore, both the *Macrocystis* density manipulation and the reef surveys suggested that the relationship between kelp bass recruitment and *Macrocystis* density was saturating at high plant densities. Because recruit density was sampled differently for reef surveys than for the *Macrocystis* manipulations, the two estimates are not comparable; reefs were sampled along transects at two discrete positions in the water column whereas manipulated plots were sampled along the length of individual plants. However, comparison of the relationship described by the reef surveys and the *Macrocystis* manipulation suggests roughly similar leveling off of recruitment as *Macrocystis* density increased. The *Macrocystis* density at which 95 percent of the asymptotic recruit density is reached was 90 and 130 stipes per 30 m^2 , for the manipulation and reef surveys, respectively.

The pattern of kelp bass recruitment among *Macrocystis* density levels was not directly related to the abundance of predators (≥ 1 year old kelp bass). Predator density was significantly greater in the highest *Macrocystis* density than the two lower density levels (Table 5, REGWF means comparison). Predator densities differed significantly among the four sampling dates, with the effect generally additive (i.e., the date by density level interaction was not significant, Table 5).

Kelp bass recruitment was strongly related to the structural complexity of *Macrocystis* (mean blade number and biomass per 0.5 m length of plant). Among plots, there was a significant positive relationship between mean density of recruits and mean blade biomass per plant (Figure 11). This increase in recruitment with greater blade biomass holds for all plant densities (Figure 12). More importantly, this relationship is not asymptotic indicating that larval recruitment is more likely limited by the availability of suitable blade surfaces on which to settle rather than by larval supply or *Macrocystis* density per se.

Blade abundance on *Macrocystis* plants does not necessarily increase with plant density. At the highest density level, *Macrocystis* plants were significantly less structurally complex (number and weight of blades) than plants at the lower two density levels. Mean blade number (± 1 SE) did not differ significantly between the low (5.4 ± 0.9) and intermediate (4.6 ± 0.5) *Macrocystis* density levels, but blade numbers at both were significantly greater than at the high density level (1.8 ± 0.3) (two factor ANOVA, $df = 8$, $F = 12.6$, $P = 0.019$, REGWF means comparison). Like blade number, mean blade biomass (± 1 SE) did not differ significantly between the low (80.2 ± 23.7) and intermediate (58.9 ± 4.1) *Macrocystis* levels, but was significantly greater for both than for the high density level (23.8 ± 1.8) (two factor ANOVA, $df = 8$, $F = 10.92$, $P = 0.024$, REGWF means comparison). Therefore, blade biomass per reef area increases proportionately with plant density to medium levels but not to high levels where plants are less structurally complex. This results in a decelerating relationship between blade biomass and plant density (Figure 13). Consequently, the asymptotic relationship between blade biomass and plant density corresponds with the same relationship for kelp bass recruits and plant density.

DISCUSSION

Spatial and temporal variation in the recruitment of larval kelp bass to local reef-associated populations was strongly related to the local abundance of the giant kelp, *Macrocystis pyrifera*. Similar relationships have been described in terrestrial systems in which plants provide microhabitats for the recruitment of insects and other plants. These systems all provide living recruitment habitats that are themselves variable in both space and time. Examples include the effect of "nurse plants" such as *Ambrosia* on the distribution of recruitment of some desert plant species (see review by McAuliffe 1988). As the effect of *Ambrosia* plants on patterns of *Larrea* recruitment persists long after individual *Ambrosia* plants vanish, so does the effect of *Macrocystis* on kelp bass recruitment well after destruction of a *Macrocystis* forest. The potential importance (i.e., contribution to recruitment dynamics) of spatial and temporal variability of such recruitment habitats could easily be overlooked. The relationship between *Macrocystis* density and kelp bass recruitment was weak when *Macrocystis* density was high and similar among reefs and kelp bass recruitment varied little from one reef to another. This result cautions against assessing the strength of relationships from correlative evidence gathered over short time periods, particularly when the independent variables such as *Macrocystis* vary greatly in time (see Dayton and Tegner 1984, Wiens et. al. 1986 for similar arguments).

In previous manipulations, the presence or absence of *Macrocystis* was shown to significantly influence recruitment of kelp bass among experimental reefs (Carr 1989). Results of the *Macrocystis* density experiment indicate that

once *Macrocystis* is present on a reef, intensity of recruitment will vary with *Macrocystis* density. The functional relationship between the local density of *Macrocystis* and kelp bass recruitment appears to be asymptotic, however. Reef surveys as well as the experimental manipulation of *Macrocystis* density revealed a nonlinear relationship and suggested that kelp bass recruitment saturates at moderate *Macrocystis* densities (ca. 100 to 130 stipes per 30 m²).

This asymptotic relationship may be due to mechanisms operating during the presettlement, settlement or postsettlement phases of the recruitment process, any one of which may involve the density dependent architecture of *Macrocystis* plants. Presettlement mechanisms of recruitment limitation involve factors that influence larval supply to a reef. One obvious interpretation of the pattern of recruitment is that there is an upper limit to the supply (i.e., density and rate of delivery) of pelagic larvae. Limited larval supply is responsible for "recruitment limitation" (Williams 1980, Doherty 1983, Victor 1983, 1986, Underwood and Denley 1984, Doherty and Williams 1988) and "supply side" population models (Roughgarden et al. 1987, Underwood and Fairweather 1989) as implied by the original use of these terms. Currently, variation in larval supply is thought to be a major determinant of reef fish recruitment (Doherty and Williams 1988). Though I did not sample larval availability to these sites directly, the linear (non-asymptotic) relationship between kelp blade biomass and recruit density indicates that larval supply was not limiting across the kelp densities (and their corresponding blade biomasses) observed in the experimental plots. Density dependent constraints on blade biomass, rather than larval supply, better explain the general asymptotic nature of the *Macrocystis* - kelp bass recruitment relationship. Certainly, larval supply may

sometimes limit local recruitment in other systems (see review by Doherty and Williams 1988 for coral reef fishes) and perhaps at other locations in the Southern California Bight. For example, a similar manipulation of *Macrocystis* density along the coast of Santa Barbara County and the Palos Verdes Peninsula revealed no such effect of *Macrocystis* density on kelp bass recruitment. During August to November, 1985 and October, 1986, I sampled 180 plants three times and 72 plants once at these two sites, where only 19 and 29 kelp bass recruits were recorded, respectively. Thus the low recruitment in the presence of dense stands of *Macrocystis*, suggests that larval supply may have been limiting at these sites.

Macrophyte density and architecture can affect larval supply to a reef and potentially cause the asymptotic pattern observed here. Increases in plant density or individual plant biomass increase drag, reduce current velocity and thereby redirect currents around a forested reef (Jackson and Winant 1983, Jackson 1986, Eckman et. al. 1989, and references in Eckman 1983, 1987). Perhaps large plants at the outer edges of *Macrocystis* beds may contribute to the leveling off of recruit densities by deflecting larvae-laden currents from, and thereby reducing larval transport to, the interior of denser *Macrocystis* stands.

If settlement involves active choice, as demonstrated for other fishes (Sweatman 1983, 1985, 1988, Marliave 1977, Sale et al. 1984), kelp bass larvae may actively bypass plants growing at higher densities because they choose not to settle on substrates of lower structural complexity (or some associated cue such as lower shade or prey availability). Recruitment of recently settled (≤ 5 day) kelp bass among algae of different structural complexity was greater on the more structurally complex alga (Carr 1991a). If this relationship reflects larval

choice, then larval preference for greater structural complexity (or associated cues) and the reduced structural complexity of *Macrocystis* at high plant densities suggest that settlement preferences may also have contributed to the asymptotic relationship.

The relationship between recruit density and *Macrocystis* density may be influenced by postsettlement mechanisms including differential survival (Shulman 1985, Shulman and Ogden 1987, Behrends 1987) and movement of fish following settlement (Robertson 1988). In addition, intraspecific competition (within and among cohorts) can influence the rate of growth of recently settled fish, though not necessarily their numerical abundance (Jones 1987, 1990, Forrester 1990). Nonetheless, reduced growth may eventually lead to increased mortality if vulnerability to predation is strongly size dependent. Indeed, density effects on growth of recently settled kelp bass within the range of natural densities have been measured (Carr 1991a). Further, strong size-related differences in vulnerability and mortality rates exist among young-of-year kelp bass (Carr 1991a).

The density of predators and the availability of shelter may have contributed to the asymptotic pattern of recruitment. When sampled, predator density was greater at high *Macrocystis* density level than at the lower densities. Field manipulations of the presence of predators (primarily ≥ 1 year kelp bass) indicate that predators can alter patterns of kelp bass recruitment (Carr 1991a). Further, recently settled kelp bass may be more vulnerable to predation in the high density stands because of the reduced structural complexity of plants there. Most canopy-forming marine and terrestrial plants may be less structurally complex at high density. This suggests that the availability of shelter or refuge

may actually decrease with increased plant density.

Within the area of my *Macrocystis* density manipulations, postsettlement movement of fish from low density to higher density *Macrocystis* stands is unlikely to have altered the pattern of recruitment very much because the presence of predators and the availability of algal-associated prey appear to greatly inhibit movement of recently settled fish among plants (Carr 1991a). Also, had post-recruitment movement among *Macrocystis* density levels occurred, it was not sufficient to alter the distribution of post-recruits established during recruitment.

Clearly, several of these mechanisms - larval supply, choice of substrate for settlement, density-dependent growth and mortality, and predator abundance and shelter availability - are directly affected by the density dependent structural complexity of *Macrocystis* measured at the experimental sites. Probably, a combination of these factors interact to limit recruitment at higher plant densities. Experimental assessment of the relative effect of each of these mechanisms will contribute importantly to our understanding of how plant habitats affect patterns of animal recruitment.

The relationship between *Macrocystis* density and kelp bass recruitment described here indicates that spatial and temporal variation in algal habitats may have strong effects on the distribution and dynamics of temperate reef fish recruitment. The strong relationship between the density of recruits and one year olds suggests that these algal effects on recruitment may have important consequences to the structure and dynamics of local open populations of kelp bass. Since immature (< 4 year old) kelp bass use similar resources as adults (Young 1963), the local density of immature individuals may reduce resource

availability thereby affecting the reproductive capacity of adults. Since macroalgae can affect the local density of recruits of a variety of temperate reef fishes in both northern (Haidorson and Richards 1987, Carr 1989, 1991b, Holbrook et al., 1990, Love et. al. 1991) and southern (Jones 1984, Choat and Ayling 1987) hemispheres, further investigation of the links between the dynamics of macroalgae and reef fish recruitment could contribute importantly to our understanding of the dynamics of reef fish populations.

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Table 1. Stepwise multiple regression models for habitat-related sources of variation of kelp bass recruitment. (A) including transects from all depths, (B) only including transects ≥ 7 m bottom depth. *Macro.* size = mean stipes per *Macrocystis* plant, *Macro.* stipes = density (stipes per 30 m^2) of *Macrocystis* stipes, *Macro.* cover = percent cover of *Macrocystis*, Depth = bottom depth, Bare rock = percent cover of algal-free rock substratum, Relief = percent cover of rock > 1 m height, *Sargassum* = percent cover of *S. palmeri*, Understory = percent cover of all understory algae combined, ≥ 1 yr kelp bass = density of older kelp bass. N = number of 30 m^2 transect samples.

Dependent variable: Density (individuals $\times 60\text{ m}^{-3}$) of kelp bass recruits.

A. ALL DEPTHS

Year	(N)	Independent Variable	Coefficient	Partial r^2	Total r^2	P
1985	(96)	<i>Macro.</i> size	1.32	0.758	0.758	0.0001
1986	(100)	<i>Macro.</i> size	0.221	0.482		0.0001
		Depth	0.225	0.063		0.0004
		<i>Sargassum</i>	0.048	0.017		0.053
		Relief	0.020	0.01		0.134
		<i>Macro.</i> stipes	0.010	0.01	0.582	0.144
1987	(101)	Depth	0.719	0.333		0.0001
		<i>Macro.</i> size	0.335	0.058		0.003
		Understory	0.119	0.055	0.446	0.002
1988	(44)	<i>Macro.</i> size	0.877	0.146		0.01
		Bare rock	-0.287	0.078	0.224	0.049
1989	(106)	<i>Sargassum</i>	0.424	0.097		0.001
		≥ 1 yr kelp bass	0.962	0.145		0.0001
		Depth	0.681	0.043	0.284	0.015

Table 1 continued.

B. DEPTH \geq 7 m

Year	(N)	Independent Variable	Coefficient	Partial r^2	Total r^2	P
1985	(28)	<i>Macro.</i> cover	0.358	0.756	0.758	0.0001
1986	(46)	<i>Macro.</i> stipes	0.038	0.566		0.0001
		Bare rock	- 0.070	0.028	0.594	0.09
1987	(47)	<i>Macro.</i> size	2.127	0.209		0.004
		Understory	0.158	0.136		0.027
		\geq 1 yr kelp bass	- 0.915	0.055		0.088
		<i>Macro.</i> stipes	- 0.117	0.081		0.003
		<i>Macro.</i> cover	0.157	0.0351		0.0001
		Relief	- 0.154	0.066	0.581	0.015
1988	(28)	Depth	1.844	0.257		0.005
		\geq 1 yr kelp bass	- 0.583	0.092		0.067
		Understory	0.148	0.081	0.43	0.071
1989	(57)	<i>Sargassum</i>	0.485	0.359		0.0001
		Sand	- 0.396	0.052		0.033
		Relief	- 0.194	0.026		0.118
		<i>Macro.</i> stipes	- 0.044	0.033	0.469	0.077

Table 2. Correlation coefficients for the three measures of *Macrocystis* recorded on annual recruitment transects and bottom depth. Data include all five years (1985 to 1989) combined. Mean plant size is the mean number of stipes per plant. Density of stipes = stipes X 30 m⁻². Canopy cover is proportion of random point contacts beneath the canopy of *Macrocystis* plants. Values in parentheses are number of transects.

	Bottom Depth	Mean plant size	Density of stipes	Percent cover
Bottom depth	1.000			
Mean plant size	0.418 (464)	1.000		
Density of stipes	0.42 (464)	0.898 (463)	1.000	
Canopy cover	0.417 (467)	0.830 (458)	0.895 (459)	1.000

Table 3. Density (fish per 10 m³) of kelp bass recruits within 1 m of the bottom in manipulated plots of each *Macrocystis* density level (low, medium and high). SE = 1 standard error. Means of log transformed (X + 0.3) recruit density are not significantly different among years or among kelp density levels (two factor ANOVA).

<u>YEAR</u>	<u>KELP DENSITY LEVEL</u>					
	<u>LOW</u>		<u>MEDIUM</u>		<u>HIGH</u>	
	<u>MEAN (1 SE)</u>	<u>MEAN (1 SE)</u>	<u>MEAN (1 SE)</u>	<u>MEAN (1 SE)</u>	<u>MEAN (1 SE)</u>	<u>MEAN (1 SE)</u>
1986	0.4	0.20	0.62	0.11	0.36	0.16
1987	0.25	0.13	0.42	0.3	0.33	0.13

TWO FACTOR ANOVA RESULTS:

<u>SOURCE</u>	<u>DF</u>	<u>MS</u>	<u>F</u>	<u>P</u>
YEAR (A)	1	0.546	1.14	0.31
KELP DENSITY (B)	2	0.16	0.33	0.72
A*B	2	0.13	0.27	0.77

Table 4. Density (fish per 30 m³) of young-of-year kelp bass 8 months after sampling of recruitment in each *Macrocystis* density level (low, medium and high). Mean log transformed ($X + 0.3$) young-of-year density is significantly different among kelp density levels. Underlined means are not significantly different from one another (REGWF means comparison). No year effect or year by kelp density interaction was detected.

YEAR	KELP DENSITY LEVEL					
	LOW		MEDIUM		HIGH	
	MEAN (1 SE)	MEAN (1 SE)	MEAN (1 SE)	MEAN (1 SE)	MEAN (1 SE)	MEAN (1 SE)
1986	2.50	0.25	<u>4.17</u>	<u>0.25</u>	<u>3.88</u>	0.75
1987	2.13	0.44	<u>2.67</u>	<u>0.18</u>	<u>3.87</u>	0.68

TWO FACTOR ANOVA RESULTS:

SOURCE	DF	MS	F	P
YEAR (A)	1	0.186	3.12	0.105
KELP DENSITY (B)	2	0.363	6.07	0.017
A*B	2	0.076	1.28	0.316

Table 5. Predator density (≥ 100 mm TL, 1 yr old kelp bass per 30 m^3) in each *Macrocystis* density level (low, medium and high) at four sampling dates. Mean kelp bass density is significantly different among dates (high > medium = low, REGWF means comparison) and *Macrocystis* density levels. No date by kelp density interaction was detected.

YEAR	KELP DENSITY LEVEL					
	LOW		MEDIUM		HIGH	
	MEAN (1 SE)	MEAN (1 SE)	MEAN (1 SE)	MEAN (1 SE)	MEAN (1 SE)	MEAN (1 SE)
OCT 86	2.93	0.68	3.93	0.41	4.67	0.58
JUN 87	2.00	0.00	1.92	0.74	3.21	0.15
OCT 87	4.71	0.44	4.79	0.79	5.54	1.01
JUN 88	2.40	0.20	3.20	0.20	4.47	0.33

TWO FACTOR ANOVA RESULTS:

SOURCE	DF	MS	F	P
DATE (A)	3	10.11	10.89	0.0001
KELP DENSITY (B)	2	6.43	6.92	0.004
A*B	6	0.32	0.35	0.903

FIGURE LEGENDS

Figure 1. Relationship between the density of kelp bass recruits and bottom depth. Plotted are the mean (± 1 SE) density of kelp bass recruits sampled at each of three categories of bottom depth (m) for each of five years.

Figure 2. Relationship between the density of kelp bass recruits and *Macrocystis* density among the five years of recruitment sampling. *Macrocystis* density increased significantly from 1985 through 1989 (single factor ANOVA, $df = 4$, $F = 24.67$, $P = 0.0001$).

Figure 3. Relationship between mean *Macrocystis* density and the relative variability (coefficient of variation) of *Macrocystis* density (solid circles) and recruit density (open circles) by year.

Figure 4. Relationship between spatial variation in *Macrocystis* density and kelp bass recruitment among reefs.

Figure 5. Relationship between temporal variation in *Macrocystis* density and kelp bass recruitment among years.

Figure 6. Relationship between the density of kelp bass recruits and *Macrocystis* density. Plotted are the mean stipe density and recruit density for approximately nine reefs in each of five years (total $n = 42$). Solid line is the best fit model.

Figure 7. Relationship between the density of recruits on a reef and the subsequent density of 1 year old kelp bass the following year (i.e., same cohort).

Figure 8. Relationship between the mean (± 1 SE) density of recruits (all reefs combined) and subsequent mean (± 1 SE) density of 1 year old juveniles the following year for each of four years.

Figure 9. Effect of *Macrocystis* density on the density of kelp bass recruits.

Plotted is the mean (± 1 SE) recruit density for six replicate plots (years combined) of each of three experimentally-created *Macrocystis* density levels. Mean recruit densities with different letters (A,B) are significantly different from one another (REGWF means comparison).

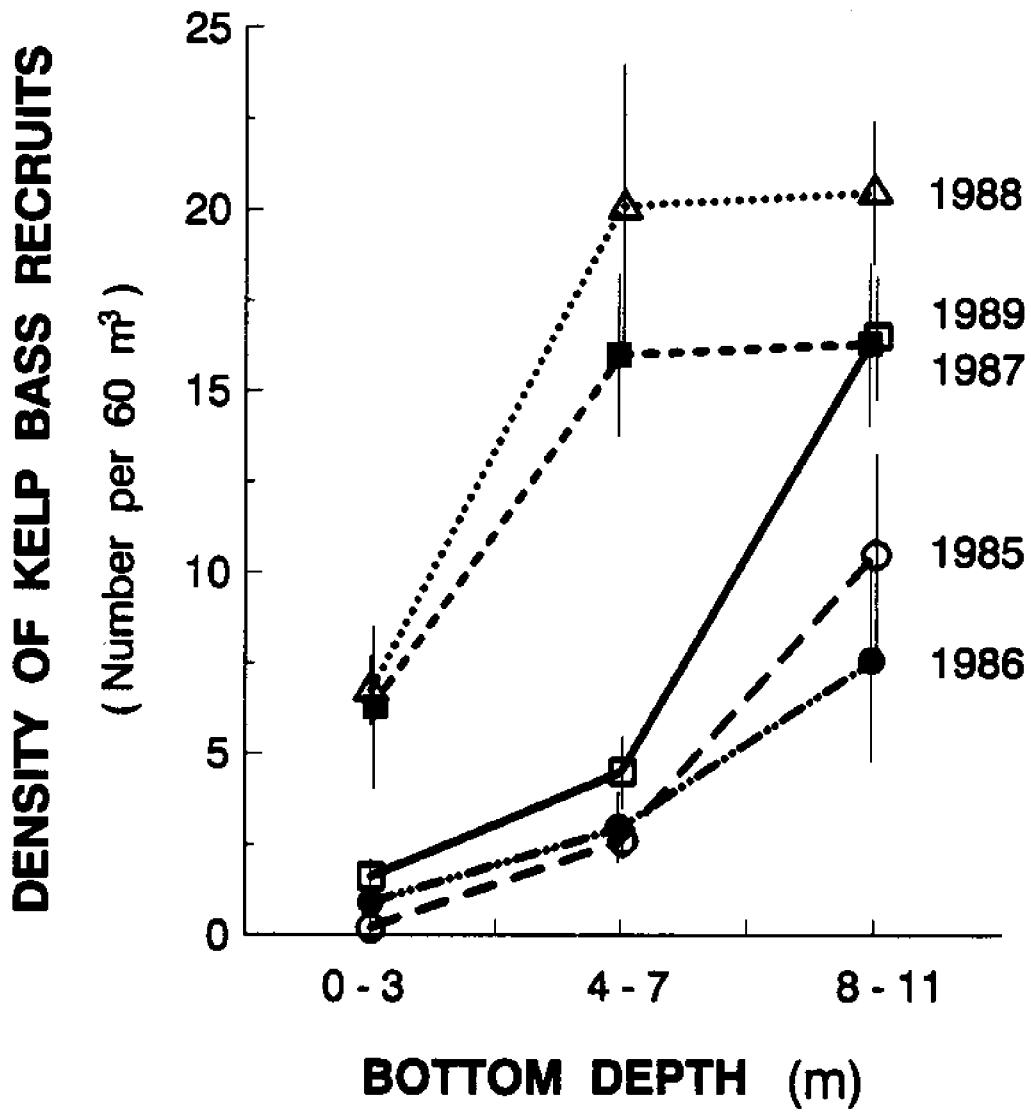
Figure 10. Relationship between kelp bass recruit density and *Macrocystis* density among the 18 experimental plots.

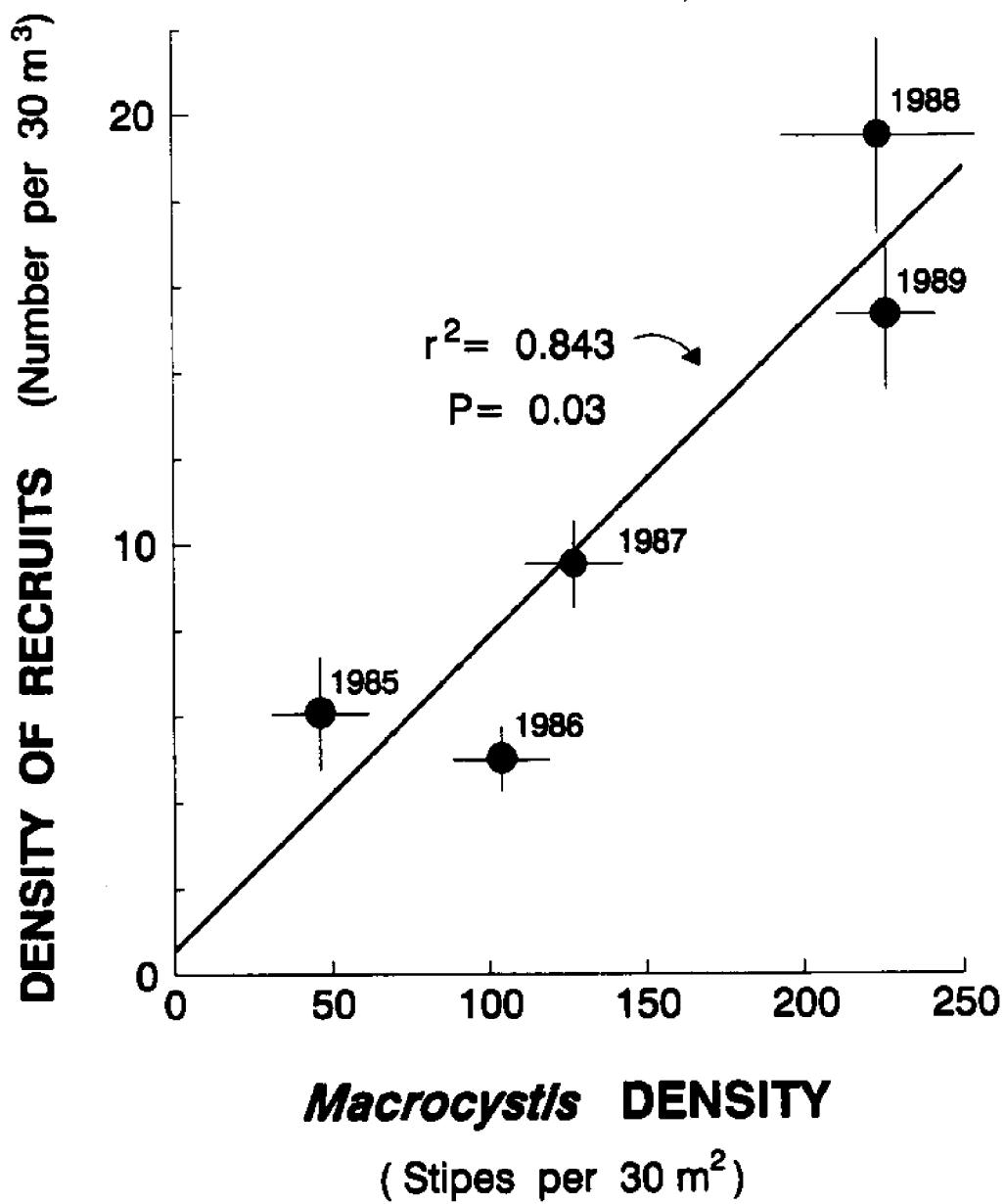
Figure 11. Relationship between mean kelp bass recruits per plant and mean blade biomass per plant. Plotted are the mean blade biomass ($n = 4$ plants) and number of recruits ($n = 8$ plants) per plant for each of the nine *Macrocystis* manipulation plots (during 1986). H, M and L refer to high, medium and low density plots, respectively.

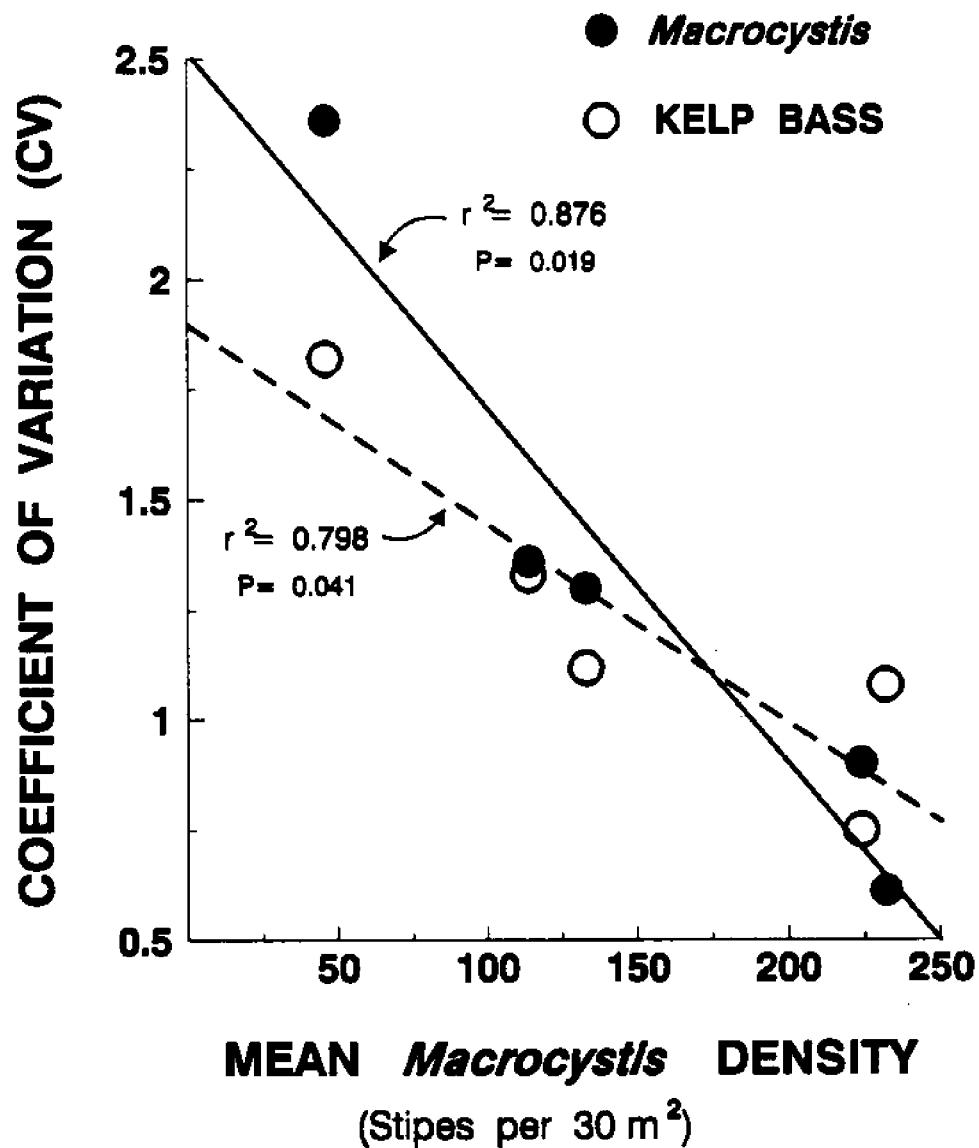
Figure 12. Relationship between mean blade biomass and mean density of kelp bass recruits for each of the nine *Macrocystis* manipulation plots during 1986. Mean blade biomass is the product of the mean blade weight per

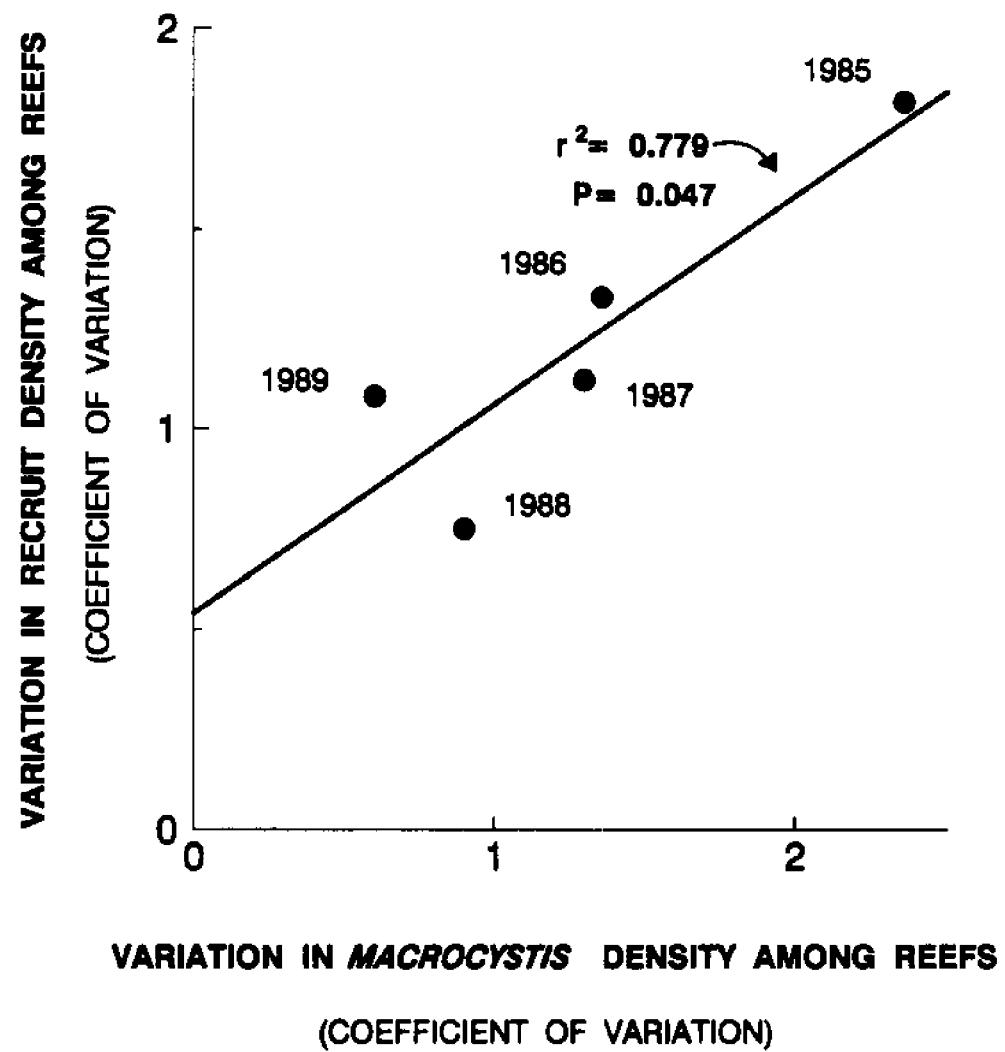
plant and plant density of each plot. H, M and L refer to high, medium and low density plots, respectively.

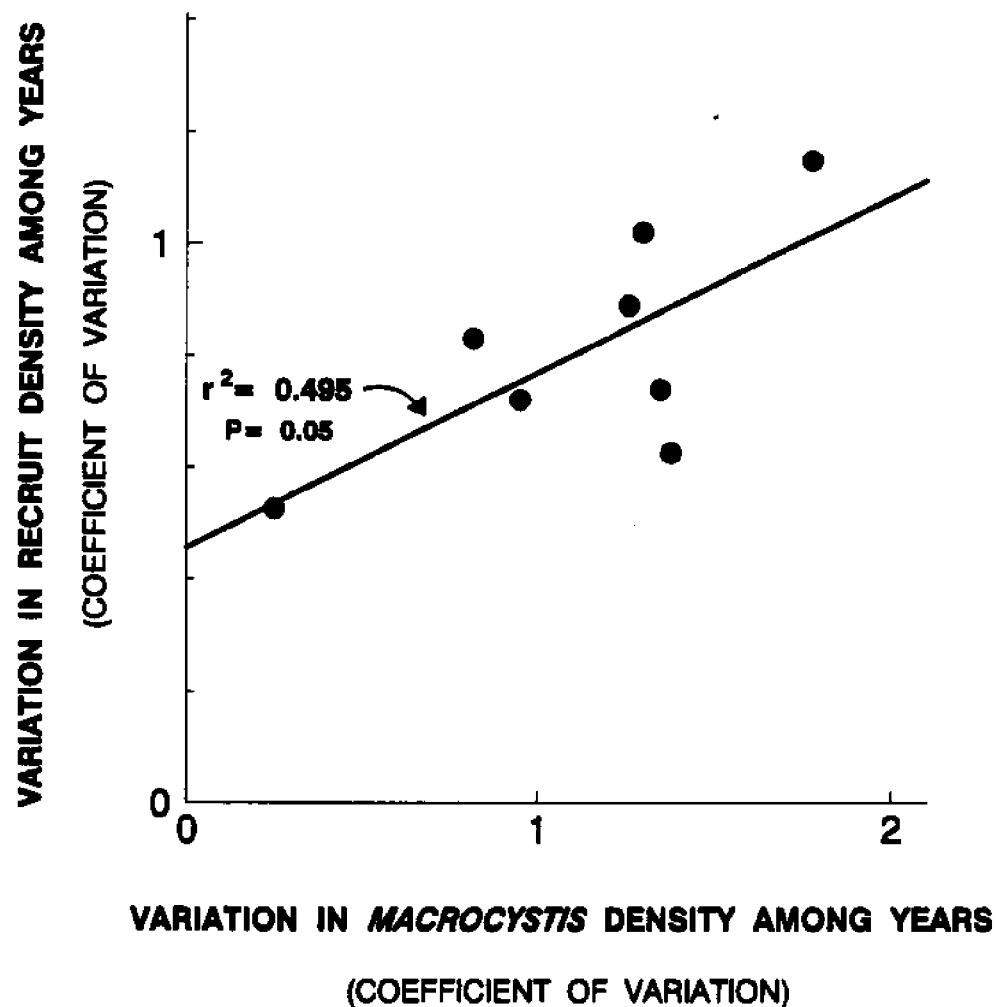
Figure 13. Relationship between blade biomass per reef area and *Macrocystis* density. Solid line describes the best fit model.

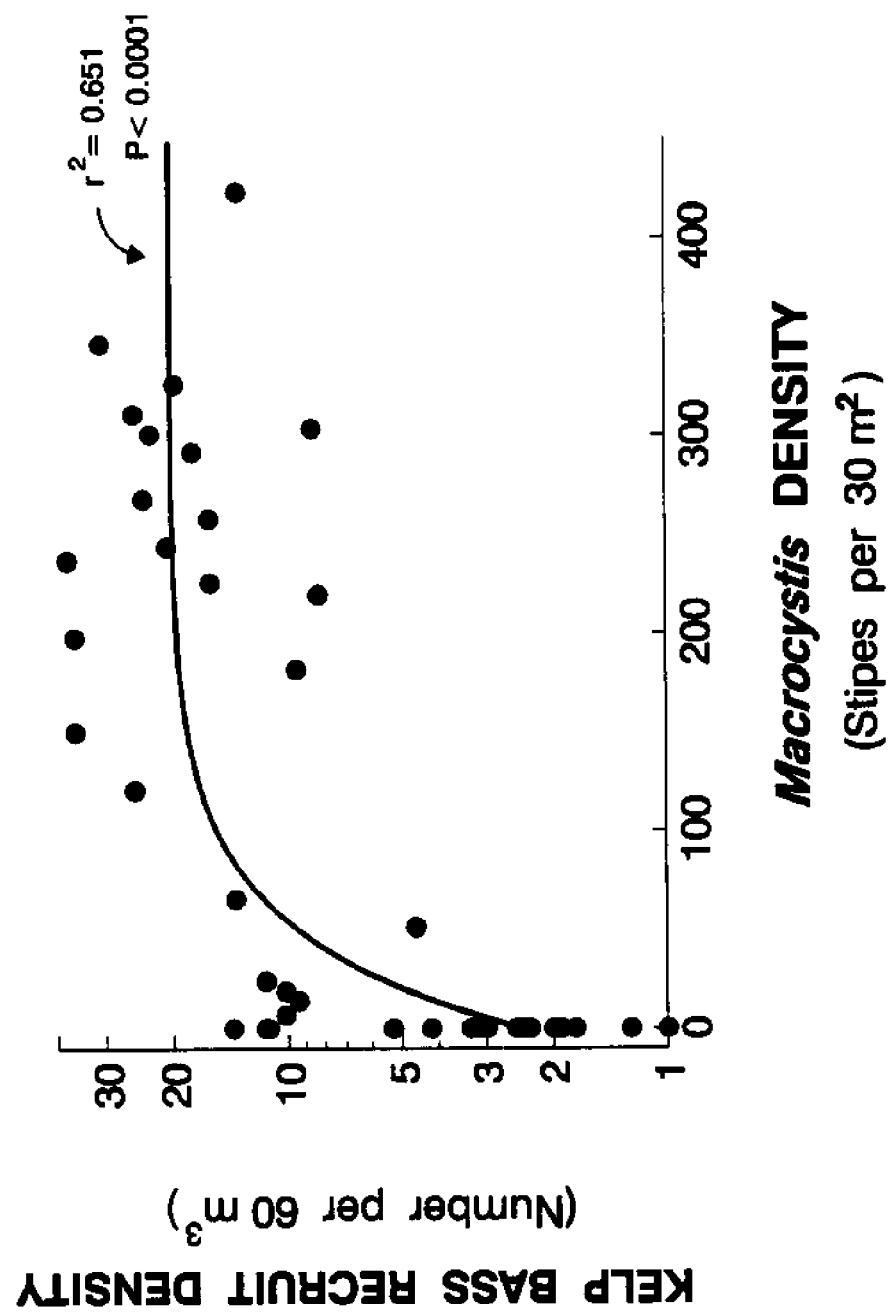


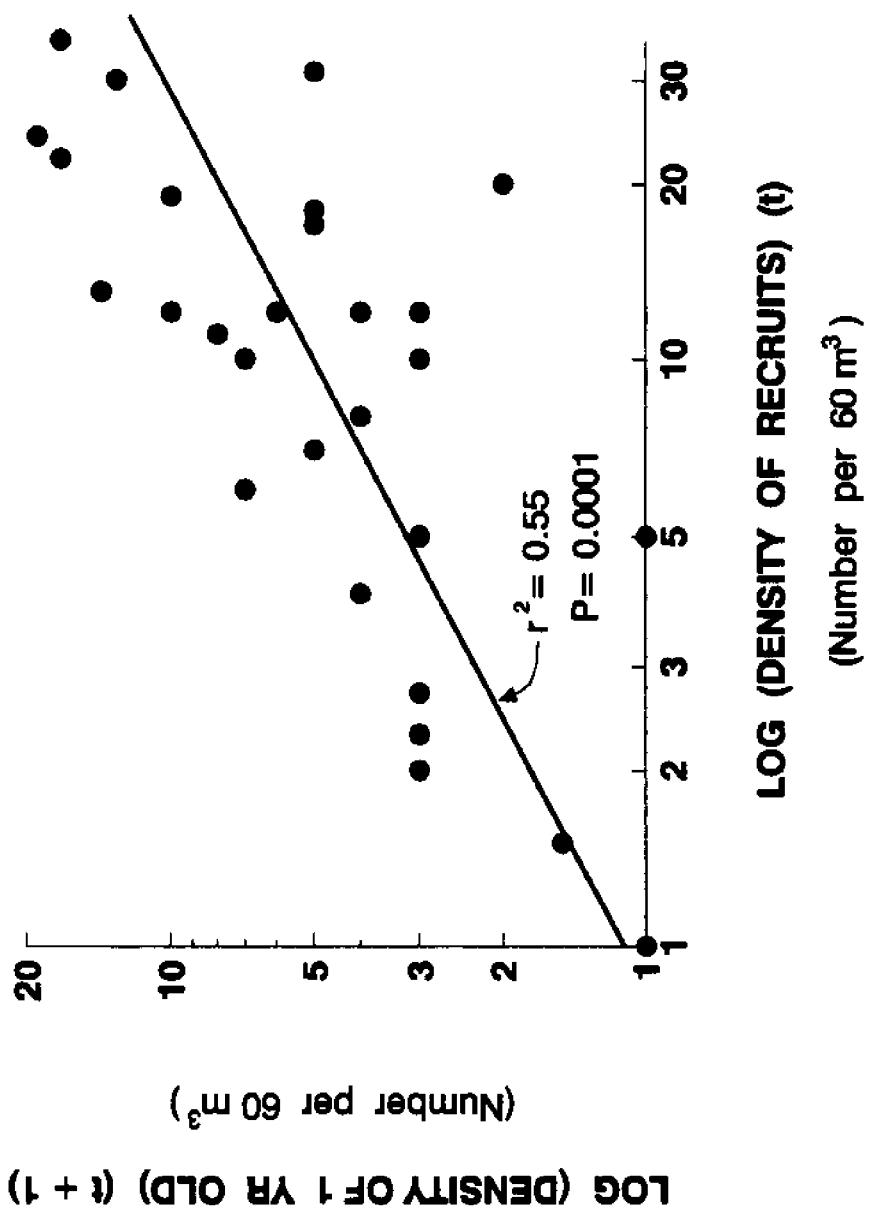


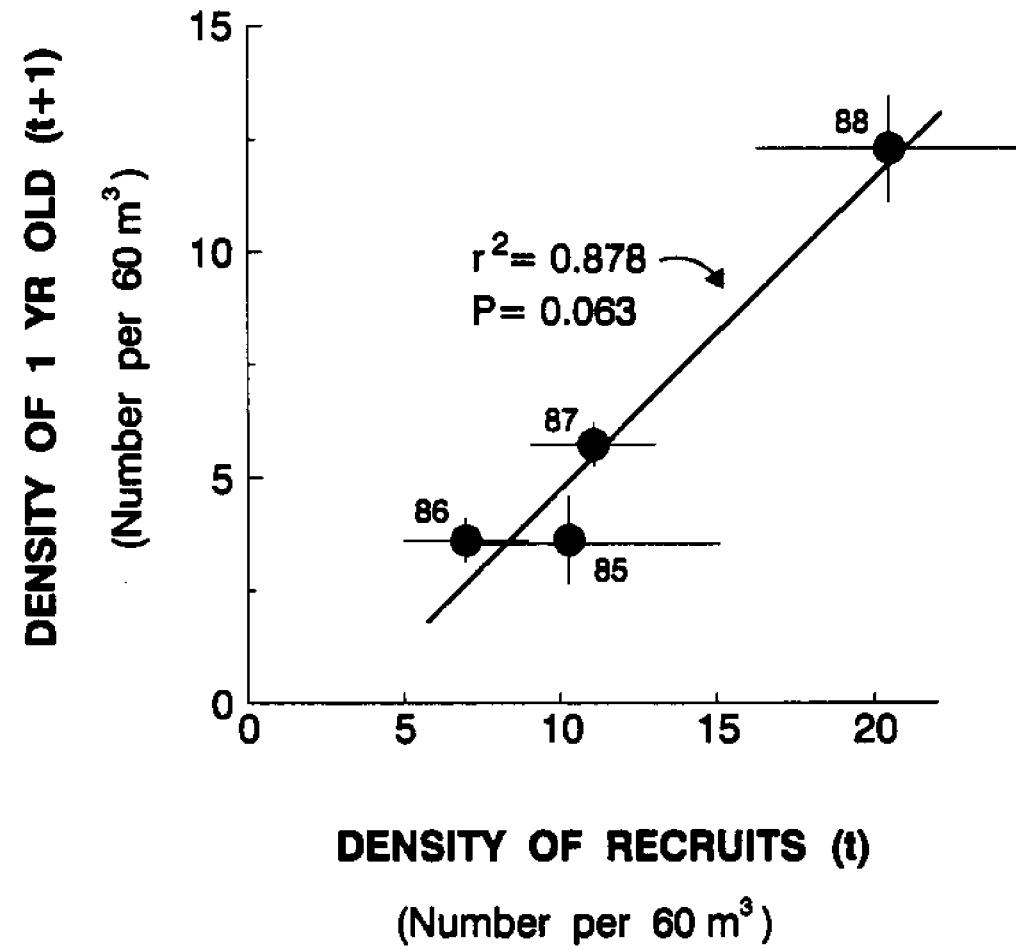


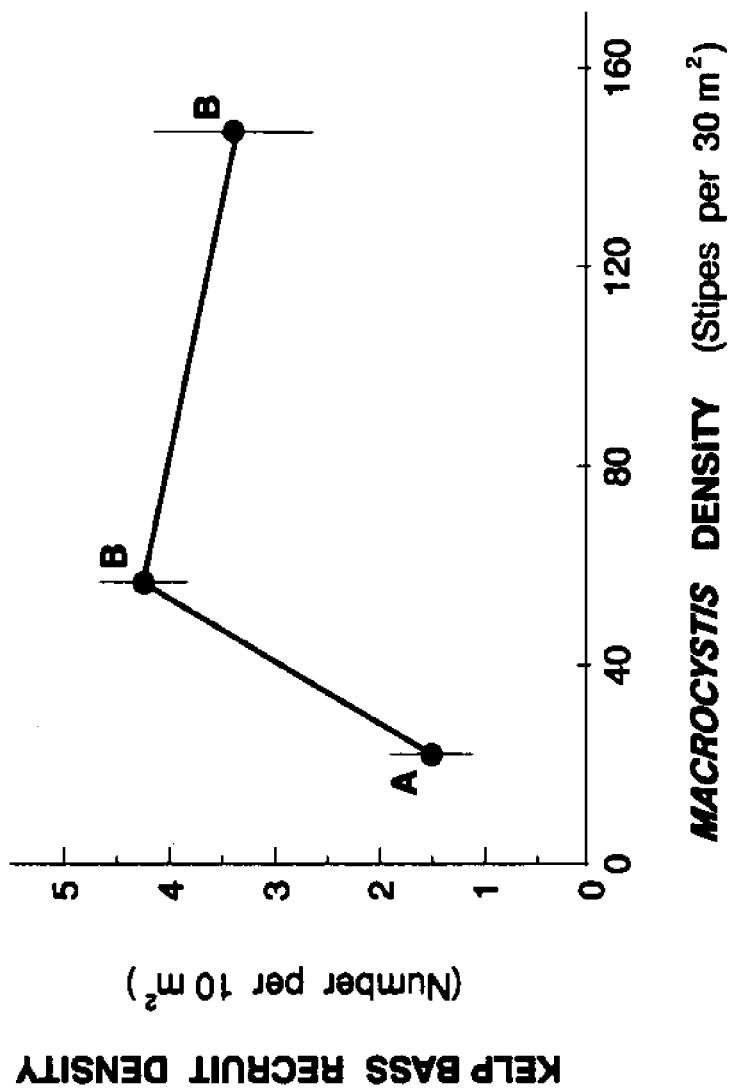


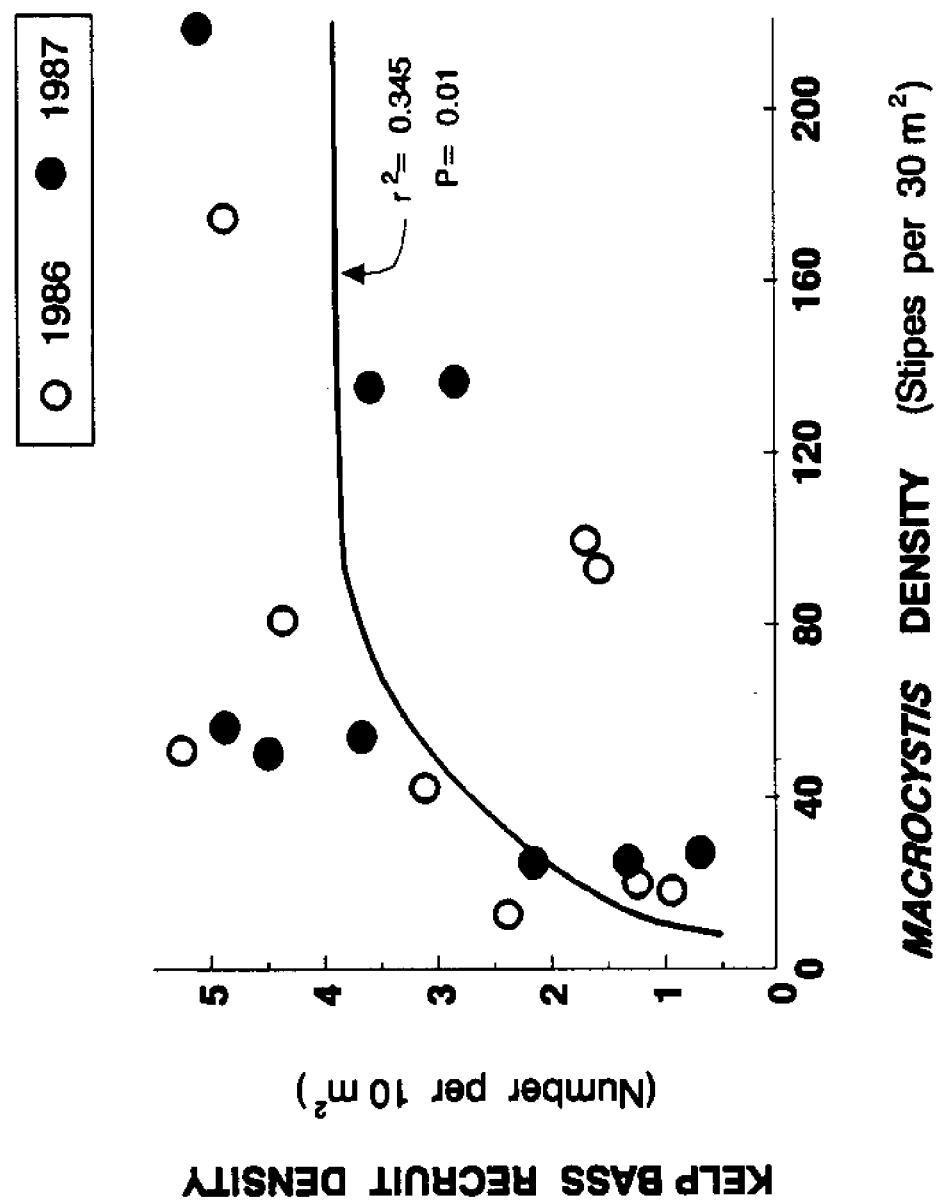


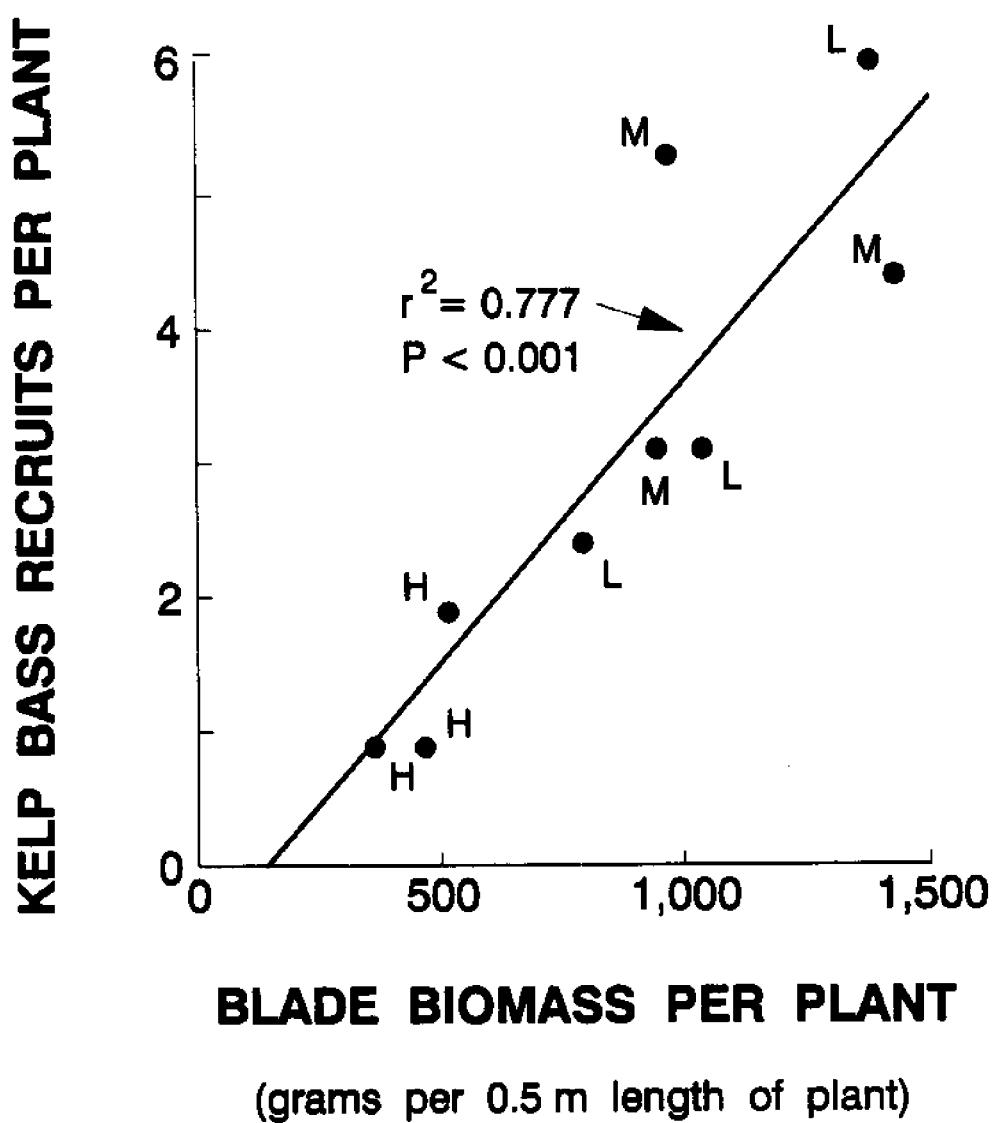


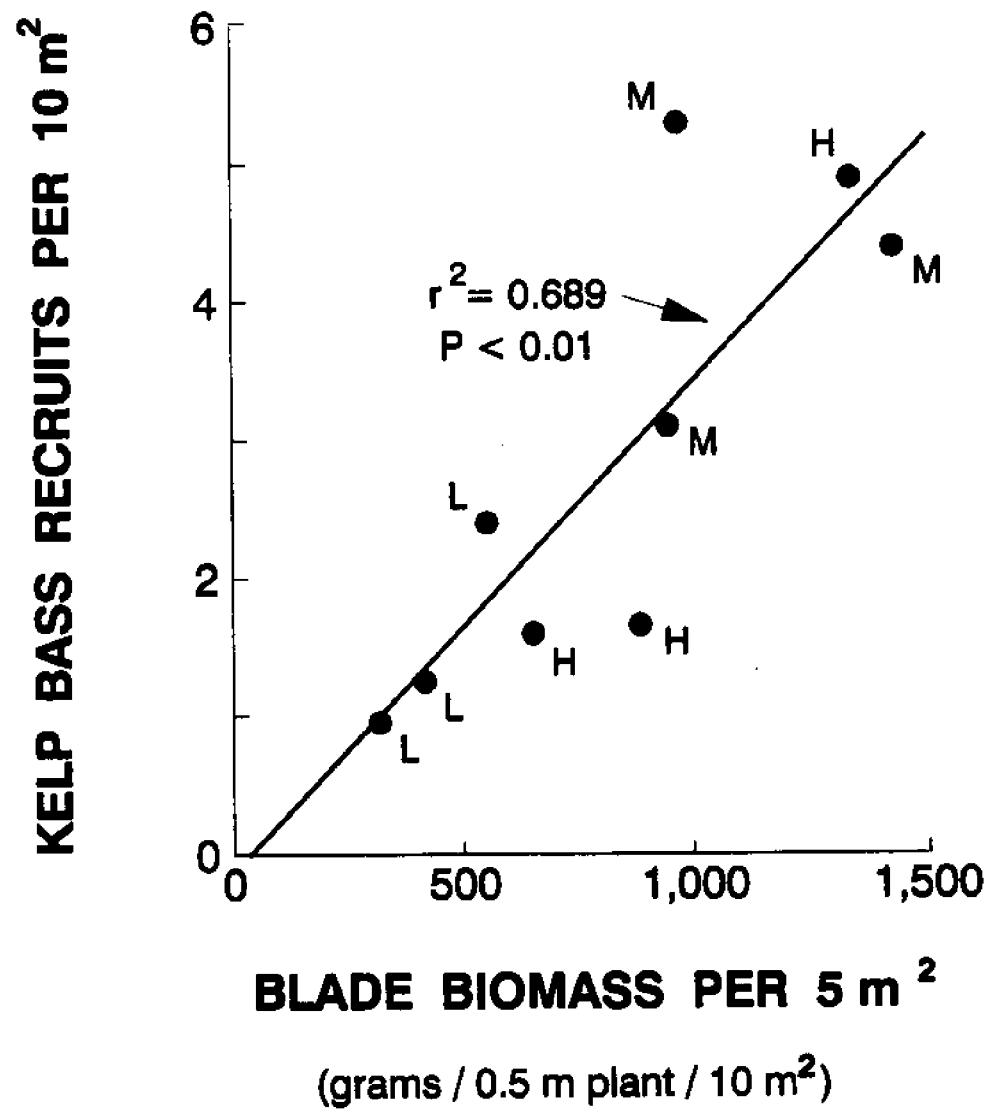


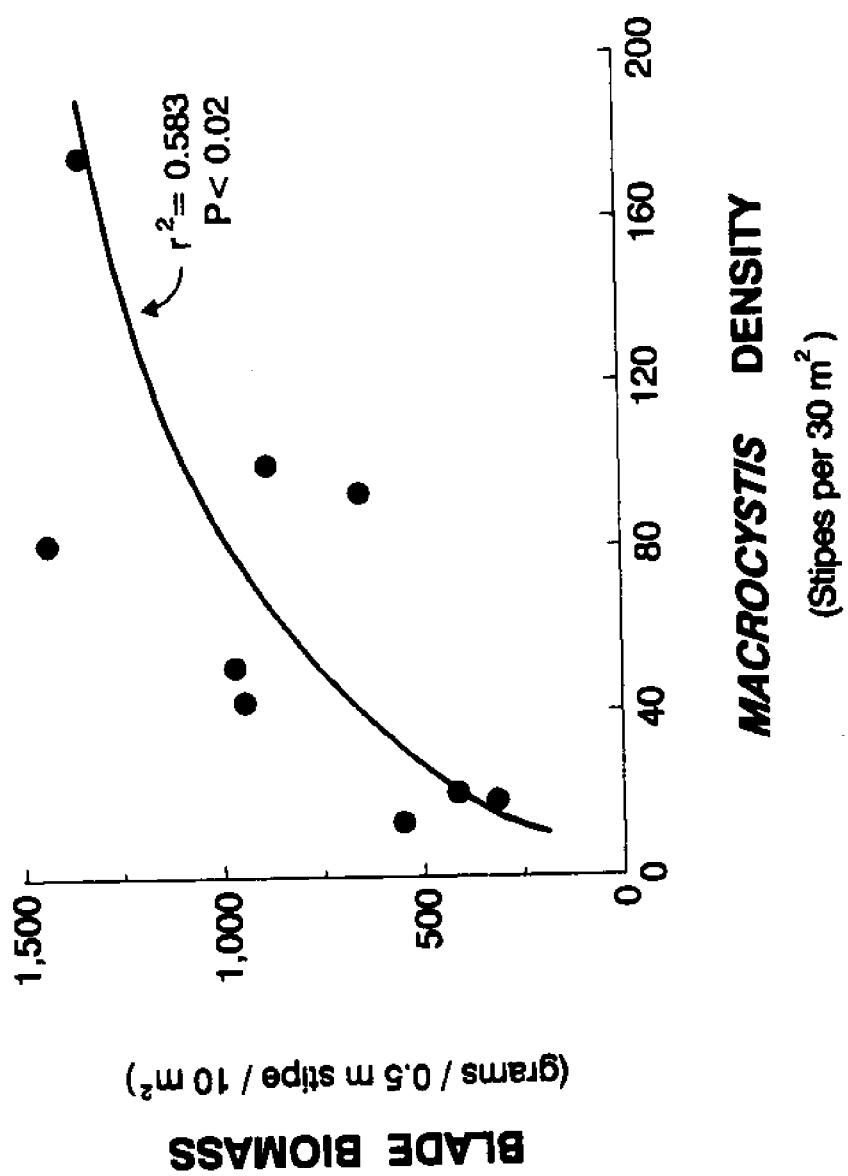












CHAPTER 2

FACTORS INFLUENCING FISH RECRUITMENT TO MACROALGAE: THE ROLE OF ALGAL HEIGHT, COMPLEXITY, AND FISH BEHAVIOR

INTRODUCTION

The spores, eggs and larvae of many marine organisms are dispersed in the plankton and often provide the major source of replenishment to local "open" populations (*sensu* Caswell 1978, Roughgarden et al. 1985). Therefore, biotic or abiotic factors responsible for variation in the recruitment of dispersive propagules may have strong effects on the dynamics of local populations of algae (Reed et al. 1988), invertebrates (Yoshioka 1982, Underwood and Denley 1984, Connell 1985, Roughgarden et al. 1985, 1988, Hughes 1990, Raimondi 1990) and fishes (Doherty 1983, Victor 1983, 1986, Doherty and Williams 1988, Forrester 1990, Jones 1990), and even the species composition of local assemblages (see reviews by Sale 1980, Doherty and Williams 1988, Mapstone and Fowler 1988, Underwood and Fairweather 1989). Factors contributing to spatial and temporal variation in propagule recruitment (*sensu* Keough and Downes 1982, Connell 1985, Doherty and Williams 1988) can occur during any of four phases of the total recruitment process: production, dispersal, settlement and the post-settlement period prior to recruitment. Estimating the relative effects of environmental factors (e.g., transport processes, resource availability, predation, etc.) and characteristics of larvae (e.g., settlement preferences, resource requirements, etc.), during each of these four phases, on recruitment variation is fundamental to our understanding of the recruitment process, the dynamics of open populations, and the structure of communities comprised of such open populations.

Marine reef fishes have been the subject of many studies addressing the role of each phase of the recruitment process in determining spatial and

temporal patterns of recruitment. Temporal periodicity of reef fish settlement has been correlated with periodicities in larval production (Robertson et al. 1988); interspecific differences in timing of recruitment may be related to the timing of larval production (Carr 1991a). Much evidence suggests that factors operating during the planktonic dispersive phase (e.g., hydrographic features, starvation, predation, etc.) strongly influence spatial and temporal patterns of settlement and recruitment (see studies reviewed by Doherty and Williams 1988, and Robertson et al. 1988). There is evidence that different reef fishes preferentially settle on different species of coral (Williams and Sale 1981, Sale et al. 1984), on substrates of different structure (Marliave 1977, Williams 1980, Sale et al. 1984), in different thermal regimes (Norris 1963), and in the presence of conspecifics (Sweatman 1983, 1985, 1988). Other factors influencing recruitment patterns during and after settlement include predation (see review by Hixon in press), shelter availability (Shulman 1985, Behrends 1987), inter- and intra-specific competition (Jones 1987, 1990, Forrester 1990) and other sources of mortality or emigration (Shulman and Ogden 1987, Robertson 1988).

Variation in the abundance and composition of algal structure may strongly influence spatial and temporal variation of fish recruitment in temperate reef systems (Jones 1984, Larson and DeMartini 1984, Haldorson and Richards 1987, Carr 1989, 1991a, 1991b, Holbrook et al. 1990, DeMartini and Roberts 1990, Love et al. 1991). This effect of algal structure is most conspicuous for several laminarian algae (i.e., kelps) characterized by tall growth forms. These species (e.g., *Macrocystis pyrifera*, *M. integrifolia*, and *Nereocystis lutea*) extend vertically through the water column from bottom depths as great as 30 m to often form dense canopies at the surface. Yet the

mechanisms responsible for this effect have received surprisingly little attention and are not well understood. Differences in recruitment of larval fish to habitats with and without such algae might reflect corresponding differences in larval availability, settlement preferences, or susceptibility to post-settlement mortality.

Here I test hypotheses accounting for the increased recruitment of kelp bass (*Paralabrax clathratus*) in the presence of giant kelp, *Macrocystis pyrifera* (hereafter *Macrocystis*). Manipulations of *Macrocystis* density have demonstrated that an increase in *Macrocystis* density causes an increase in local kelp bass recruitment (Carr 1989, 1991b). This effect of *Macrocystis* is reflected in the spatial and temporal variation in kelp bass recruitment within and among rocky reefs at Santa Catalina Island (Carr 1989, 1991b). In the absence of *Macrocystis*, reefs at Santa Catalina Island support dense stands of shorter (< 1 m tall) algae, a pattern typical of reefs throughout southern California and over the main range of kelp bass (Dayton et al. 1984, Dayton 1985, Reed et al. 1988).

Here I examine several hypotheses that may account for differences in local recruitment between habitats dominated by *Macrocystis* and habitats containing mostly shorter algae. I address the following questions: (1) are planktonic kelp bass larvae available to settle in reef habitats lacking *Macrocystis*? (2) when given a choice, do kelp bass preferentially settle on *Macrocystis*? (3) does the greater height of *Macrocystis* influence the relative number of kelp bass recruiting to this alga? and (4) how does the structural complexity of a plant influence kelp bass recruitment?

METHODS

I. Patterns of abundance of recently settled kelp bass on different algal species.

To characterize the algal assemblage available for kelp bass settlement in areas lacking *Macrocystis*, the relative cover of algae was determined at random points along 30 m band transects (60 points per transect). Estimates of mean percent cover per transect were calculated from 193 transects, sampled in shallow (5 to 11 m depth) reef areas lacking *Macrocystis*. As determined from these estimates of algal composition, the predominant algae (> 10% cover) were sampled for kelp bass recruitment and used in the experiments described below.

I sampled young (< 20 mm standard length) kelp bass on the six most abundant species of algae (*Cystoseira osmundacea*, *Dictyopteris* spp., *Eisenia arborea*, *Macrocystis pyrifera*, *Sargassum palmeri*, and *Zonaria farlowi*) that grew within the depth range of kelp bass settlement (ca. surface to 12 m). Sampling was conducted along the northeast shore of Santa Catalina Island (33°27'N:118°29'W) during the main period of kelp bass settlement (August and September) from 1984 to 1988. I estimated the abundance of recently settled kelp bass by collecting samples of algae and examining them in the laboratory for larvae. Algae were gently removed from the substratum (at the holdfast) and collected in 0.5 mm mesh Nitex bags. Each sample was immersed and agitated in fresh water to remove recently settled kelp bass and, then weighed damp.

II. Larval availability in reef habitats lacking *Macrocystis*.

To determine if lower recruitment to reef areas lacking *Macrocystis* was due to a paucity of larvae available to settle, I sampled larvae in the water column above such areas examining recruitment to "larval collectors" at six reefs varying in exposure to currents. Two larval collectors were suspended at each of two depths in the water column (1 m below the surface and in the middle of the water column = mid-depth) at each site. Each collector consisted four bundles, each of a standard weight of *Sargassum palmeri* (mean \pm 1 SD = 1.825 ± 0.001 kg) enclosed in a 2.5 cm mesh nylon bag. *Sargassum palmeri* was used as a settlement substrate because it collects more fish per unit volume than all other algae tested (see Results: algal selection section). Larval collectors were placed in the field on August 27 and 28, and retrieved 15 days later by carefully removing them from lines and immediately enclosing them in 0.5 mm mesh Nitex bags underwater. In the laboratory, the alga was rinsed in freshwater and the rinse water sieved (0.5 mm mesh) for larvae.

III. Vertical distribution of kelp bass recruitment on *Macrocystis* plants.

The greater recruitment of kelp bass to *Macrocystis* may arise from settlement of larvae that encounter *Macrocystis* in the upper portions of the water column. Therefore I examined kelp bass recruitment along the entire length of *Macrocystis* plants to determine whether the number of recruits varied at different depths. From August 9 to September 8 1985, 18 *Macrocystis* plants were sampled weekly for recruits . Each plant was visually searched from

surface to bottom and the numbers of recruits to the plant in the upper, middle and bottom third of the water column were recorded.

Because older (larger) recruits may move among vertical portions of a *Macrocystis* plant and thereby obscure patterns of settlement, I estimated the size and depth distribution of recruits by collecting and measuring the standard length (mm SL) of fish at three depths on 9 randomly selected plants each week.

IV. Effect of height in the water column and orientation of algae on kelp bass recruitment.

Because recruiting kelp bass were found along the entire length of *Macrocystis* plants in the field (see Results; vertical distribution section), I conducted two experiments to determine the effect of height (upper, middle and bottom portion of water column) and orientation (extending vertically up into the water column vs. horizontally along the bottom) of plant structure on the magnitude of recent settlement of kelp bass.

I first estimated kelp bass recruitment to parcels of algae of similar volume and biomass suspended in the upper, middle and bottom portions of the water column. This isolation of parcels at different depths was intended to prevent post-settlement movement from one depth to another, so as to more precisely reveal the vertical distribution of larval settlement (and post-settlement survivorship). Because the effectiveness of different algae in collecting settling kelp bass was not known, I used two species, *Sargassum palmeri* and *Eisenia arborea*, which were suspended on separate buoyed lines and interspersed in position. Parcels of each species were suspended at each of

three depths (1 m below the surface, midway between the surface and bottom, and 1 m above the bottom) on eight lines (i.e., 4 parcels per depth per species) buoyed over a featureless sand bottom (depth = 8 m). Parcels were cleaned of associated organisms by immersion in freshwater, and were standardized by biomass prior to deployment in the field. Volume (m^3) of the parcels was estimated in the field from measurements of their height and two perpendicular widths after they were attached to the buoyed lines. The 8 lines were placed parallel to shore and separated by 5 m from one another. At the end of 20 days, algae were collected in 0.5 mm Nitex bags, rinsed, and sieved to collect larvae as described above. This experiment was repeated and the trials used as replicates ($n=2$) for comparison of recruitment among locations in the water column and algae.

Kelp bass recruits were pooled among plants for each depth and trial. Percent recruitment was transformed (arc sine-square root) and compared between algal species and depths with a two factor ANOVA and REGWF a posteriori means comparison using trials as replicates.

To determine if algae extending vertically through the water column supported greater kelp bass recruitment than algae extending horizontally along the bottom, I compared recruitment to similar masses of *Sargassum palmeri* deployed in these two orientations isolated over a featureless sand bottom. Each mass consisted of 16 parcels of *Sargassum*, in a square matrix 4 by 4, 6 m on a side. One matrix extended vertically up into the water column from 1 m above the bottom to 1 m below the surface. The other matrix extended horizontally on the bottom. Parcels of *Sargassum* were rinsed in freshwater to remove associated organisms and standardized by weight (mean \pm 1 SD (kg):

Trial 1 = 0.86 ± 0.008 , Trial 2 = 0.94 ± 0.02) prior to placement in the field. Two sets of paired vertical and horizontal matrices were deployed, one set located approximately 10 m distant from and offshore of the other. This design was repeated for two trials each consisting of 10 days of exposure to larval settlement (July 25 to August 4 and August 10 to 20, 1988). Algal parcels were collected, rinsed and sieved for larvae as described above. I compared the total number (i.e., frequency) of recruits per matrix in a three factor (orientation, trial and location), log-linear contingency analysis (SAS).

V. Field tests of algal selection by kelp bass recruits.

To determine if some characteristic of *Macrocystis* other than simply its presence throughout the water column *per se* contributed to the greater recruitment of kelp bass to *Macrocystis* than to other algal species, I suspended similar volumes of four different plant-like substrates at the same depth and compared recruitment to each over a 14 day period of exposure to settlement. The four substrates consisted of the species *Eisenia arborea*, *Sargassum palmeri*, *Macrocystis pyrifera*, and an artificial plastic mimic of *Macrocystis*. The four substrates were distributed at two depths (mid-depth = half the distance to the surface from the bottom, bottom = 1 m above the bottom) on each of 25 buoied lines arrayed in a 5 by 5 matrix (5 m between adjacent plants). Substrate types were allocated to lines in a Latin square design, each type being represented once in each row of the matrix, independently for each of the two depths. At the end of the 14 day trial, substrates were collected in 0.5 mm Nitex bags, rinsed, and sieved for larvae as described above. I standardized for substrate

volume (recruits per 0.1 m^3) and compared total kelp bass recruits among substrate types by a chi-square analysis using as expected values a uniform distribution of recruits among substrates.

VI. Laboratory tests of preference by recently settled kelp bass for different algal species.

To determine if increased recruitment in the presence of *Macrocystis* is augmented by a behavioral preference for *Macrocystis* by kelp bass, I tested for algal preference of recently settled kelp bass in the laboratory between *Macrocystis* and the three most abundant alternative algae. Similar numbers of kelp bass of sizes at settlement (10 to 20 mm SL) were collected from *Macrocystis* and *Sargassum* and pooled in laboratory aquaria. A single individual was released into a 3.1 m^3 (1 m deep X 2 m dia) aquarium in which four clumps of algae (*Dictyopteris sp.*, *Eisenia arborea*, *Macrocystis pyrifera*, and *Sargassum palmeri*) of similar volume (approx. 0.03 m^3) were anchored evenly around the perimeter. Algal positions were reassigned between trials to prevent directional and position (adjacent algae) effects. Kelp bass were suspended at the surface in the center of the tank in a clear plastic bag for 5 to 10 min prior to release in order to acclimate fish to the experimental conditions. Upon release, the fish was observed continuously for 20 min and two variables were recorded: number of minutes spent within 5 cm of each alga or the open water, and number of visits among algal clumps. Because environmental conditions (e.g., time of day, algal-associated food, presence of predators) might influence a fish's affinity toward an alga, algal preference was tested under five conditions

to compare the effects of time of day, state of hunger, presence of algal-associated food, and presence of predators.

To test for an effect of diel period on algal selection, algal selection was compared between mid-day and evening crepuscular (post-sunset) trials. To test for an effect of hunger state on algal selection, trials were compared using individuals fed within the hour and individuals starved for 24 hr. To test for an effect of algal-associated food (primarily crustaceans) on algal selection, trials were run with algae on which prey were kept intact and algae from which prey were rinsed with freshwater. Prey were kept intact on plants by collection and transfer of plants to aquaria within 0.5 mm mesh Nitex bags. To test for an effect of predator presence on algal selection, trials were conducted with and without 5 one yr old kelp bass contained in glass jars dispersed among the algal clumps. Jars were placed so as not to interfere with movement of the test animal between adjacent plants.

To test for preferential affinity for *Macrocystis*, I compared the mean proportion of time spent with *Macrocystis* with that expected given random association among the four available algae (0.25) under each of the five conditions separately. To test the effect of the four variables described above on preference for *Macrocystis*, the proportion of time spent with *Macrocystis* was compared among all five experimental conditions. I also tested the effect of the five conditions on affinity toward algae in general (all species combined) and on movement, recorded as the number of visits to different patches of algae during the 20 min trial. Preference for *Macrocystis*, affinity for algal structure and movement were compared among the five experimental conditions with a single-factor ANOVA. Proportion of time and number of visits was arc sine-

square root and log ($X + 1$) transformed, respectively, prior to analysis.

VII. Effects of structural complexity and natural substrate on recruitment of kelp bass.

The most structurally complex alga, *Sargassum palmeri*, often experienced the highest recruitment of algae I tested in the field under similar conditions (volume and position in the water column). Therefore, I tested for the effect of structural complexity on algal selection by kelp bass recruits by comparing recruitment between a structurally complex (*Sargassum*) and simple (*Macrocystis*) alga of similar weight and volume. I also tested simultaneously for the effect of substrate type (natural versus artificial) of similar complexity to explore the relative effect of substrate type and structural complexity on patterns of recruitment.

To control for larval encounter rates, I randomly interspersed two parcels each of natural *Macrocystis*, a plastic mimic of *Macrocystis*, natural *Sargassum*, and a plastic mimic of *Sargassum* which were standardized by weight and volume. To control for post-settlement movement and predation, parcels were isolated at mid-depth in the water column (depth = 5 m) above a sand bottom (depth = 13 m). Isolation in the water column was intended to reduce predator encounters and post-settlement emigration of recently settled kelp bass so that recruitment would more closely reflect settlement patterns. Predators (older kelp bass) were never observed at the isolated algal parcels. The process was repeated over 5 trials. Exposure periods varied among trials (3

to 5 days). Mean recruits per day was compared among complexity levels (high vs low), substrate type (natural vs artificial), and trial (5) using two parcels each trial as replicates ($n=2$) in a three factor ANOVA.

RESULTS

I. Patterns of abundance of recently settled kelp bass on different algal species.

In the absence of *Macrocystis*, algal cover is dominated by four species at Santa Catalina Island; *Sargassum palmeri*, *Dictyopteris* spp., *Zonaria farlowi*, and *Cystoseira osmundacea* (Table 1). Another species, *Eisenia arborea*, which is predominant at depths less than 5 m, above the shallowest transects sampled for algal cover. Therefore, *Eisenia* was also sampled for abundance of recently settled kelp bass.

Few, if any, recent settlers were collected on each of the four algal species in the absence of *Macrocystis* (Table 2). The numbers of individuals per kg alga were about two orders of magnitude less than in samples collected from the upper portions of *Macrocystis* plants. Therefore, the low numbers of kelp bass recruits at the end of the settlement period in habitats lacking *Macrocystis* (Carr 1989, 1991b) probably simply reflects a low number of early settlers in these algae, perhaps resulting from lower larval supply to those reefs, lower settlement, or very early post-settlement mortality.

II. Larval availability in reef habitats lacking *Macrocystis*.

Larvae are indeed present in the water column at reef sites lacking *Macrocystis* (Table 3). Kelp bass recruitment (number per kg algae) to the larval collectors placed in the upper water column greatly exceeded recruitment to natural substrates (Table 2). Furthermore, recruitment to the larval collectors exceeded recruitment to the upper portions of *Macrocystis* at all six sites (Table 2). This suggests that larval availability at sites lacking *Macrocystis* is probably as high as at sites with *Macrocystis*. Therefore, differences in density of recently settled kelp bass and annual recruitment between sites with and without *Macrocystis* are not related to differences in larval availability. Rather, such differences are more likely to be due to differences in settlement rates and/or early post-settlement survivorship.

III. Vertical distribution of kelp bass recruitment along *Macrocystis* plants.

Weekly censuses over the length of *Macrocystis* plants indicated that most early kelp bass recruits were in the middle and upper portions of the plants (Figure 1). Over the one month sampling period, the relative abundance of recruits declined in the surface portion as it increased in the bottom portion. This pattern suggests that either differential mortality between vertical strata occurs or that fish move from the upper to lower portions of plants. A gradual shift in recruit size from smaller to larger individuals in these plants represents growth of individuals comprising this cohort over the one month sampling period (Figure 2). Taken together, these data suggest that initial recruitment is

greatest in the upper two thirds of *Macrocystis* plants, but that the abundance peak shifts to the middle and bottom portions of plants as fish grow older.

IV. Effect of height in the water column and orientation of algae on kelp bass recruitment.

The vertical position of an alga in the water column strongly influenced the magnitude of kelp bass recruitment (Table 4). Both algae *Sargassum* and *Eisenia* had similar recruitment densities and similar recruitment patterns among vertical strata (i.e., no significant alga by depth interaction). Mean recruitment at mid-depth was approximately twice as great as that at the surface and bottom portions of the water column. These results suggest that a tall alga like *Macrocystis* oriented vertically in the water column would collect more settlers than a similar mass of short algae spread over the bottom.

Vertically oriented algae did in fact collect 2 to 3 times recently settled kelp bass than did similar amounts of algae distributed horizontally along the bottom (Table 5). Although kelp bass recruitment tended to be greater at the offshore plots (location effect: $P = 0.07$) and differed significantly between the two experimental trials (trial effect: $P = 0.02$), these effects were generally additive (i.e., no significant two or three factor interactions were detected).

V. Field tests of algal selection by kelp bass recruits.

Over the 14 day period of exposure, kelp bass settled from the plankton to all four algal substrates suspended in the water column (Table 6). However,

recruit density (per volume) differed among the four substrates. *Sargassum* had higher and artificial "*Macrocystis*" lower densities than expected. Importantly, recruitment to natural *Macrocystis* was no greater than expected, exceeding only that to its artificial mimic. These results indicate that kelp bass will settle and recruit to a variety of algal substrates if distributed similarly through the water column. Therefore, greater overall recruitment to *Macrocystis* may not reflect a strong behavioral preference of settlers for *Macrocystis per se* but to its greater height in the water column.

VI. Laboratory tests of preference by recently settled kelp bass for different algal species.

Across all five experimental regimes under which substrate preference of newly settled kelp bass was tested (varying hunger state, time of day, predator and prey occurrence), individuals never exhibited a strong preference for *Macrocystis*. Under no condition did recently settled kelp bass spend more than 25% of the time near *Macrocystis* than expected by random association among the four algae present (Figure 3, T-test: $P = 0.1, 0.5, 0.6$, and 0.96 for regimes A, C, D, and E, respectively). The only significant deviation from random was a lower than expected association of starved fish with *Macrocystis* in the absence of predators (Figure 3, regime B, T test: $P = 0.0001$). Further, there was no detectable difference in the proportion of time spent on *Macrocystis* across the five experimental regimes (Single-factor ANOVA; $df = 4$, $F = 1.24$, $P = 0.30$).

However, I detected subtle effects of the presence of their predators and of the algal-associated prey on the affinity of fish for algae in general and fish

movement. Movement of recently settled kelp bass, measured as the number of visits among algae, differed among the five regimes (Figure 4, single-factor ANOVA: $df=4$, $F = 8.2$, $P = 0.0001$, REGWF means comparison). Two factors, hunger state (A vs B regimes) and time of day (C vs D regimes) had no detectable effect on movement of recent settlers. The presence of predators (A vs C regimes) strongly reduced movement of the recent settlers among algae. The presence of food on algae (B vs E) tended to reduce movements, although not significantly so.

Affinity for algae in general (measured as percent time spent within 5 cm of all algal species combined), was strong in all five regimes, but the degree of affinity differed among regimes (Figure 4, single-factor ANOVA: $df=4$, $F = 11.9$, $P = 0.0001$, REGWF means comparison). Fed fish in both the absence of predators and of food on algae (regime A) occupied algal clumps significantly less than in all other cases. Hungry fish in both the presence of predators and of algal-associated prey (regime C), a regime most similar to natural conditions in the field, were almost always observed within algal clumps. All fish under the remaining three regimes -- either starved or with predators or with prey on algae (B,D, and E, respectively) -- spent 85 to 90 percent of their time associated with algae.

VII. Effects of structural complexity and natural substrate on recruitment of kelp bass.

Both the complexity and type (artificial vs natural) of settlement substrate affected kelp bass recruitment (Table 7). Recruitment was

significantly greater on the more complex substrates, whether artificial or natural, and significantly greater on natural substrates, whether of complex or simple structure. The fact that there was no significant complexity by type interaction and that both variables explained similar amounts of variation suggested that their relative effects were similar. Thus, these results explain the observed greater recruitment to *Sargassum* than to less structurally complex algae like *Macrocystis* under comparable conditions (i.e., similar volume and height in the water column). In addition, they suggest that some characteristic of natural algae -- perhaps a chemical attractant or presence of associated food -- enhances the complexity effect. It is unlikely that the artificial structure leached a chemical deterrent of some sort because both plastic substrates were soaked in running seawater for several weeks prior to the experiment.

DISCUSSION

Although larval supplies to habitats with and without *Macrocystis* were not directly measured in this study, the large numbers of planktonic kelp bass collected from the water column over reefs lacking *Macrocystis* were equal to or even greater than numbers collected from *Macrocystis* plants. Even though larval abundance varied as much as two-fold among sites lacking *Macrocystis*, this variation in larval availability is small relative to the five-fold increase in recruitment observed between adjacent areas with and without *Macrocystis* (Carr 1989, 1991b). Thus, the lower kelp bass recruitment to sites lacking *Macrocystis* at Santa Catalina Island is probably not due to limited larval

availability. At larger (regional) scales, however, differences in kelp bass recruitment among sites all supporting dense stands of *Macrocystis* in one place or another probably reflect differences in larval availability over larger areas (Carr 1991b).

My experimental results indicate that two factors -- affinity of larval and post-larval kelp bass for algal structure *per se* and the presence of a tall alga such as *Macrocystis* -- can account for differences in kelp bass recruitment between habitats with and without *Macrocystis*. Although kelp bass recruited throughout the length of *Macrocystis* plants, the relative number of early recruits was greater in the upper and middle portions than in the lower. Recruitment to parcels of algae positioned at different heights in the water column over a featureless sand bottom (which likely discouraged post-settlement movements and minimized any dilution of larval abundance from settlement onto nearby algae) indicated that recruitment was greatest at mid-depth. Likewise, recruitment was greater to algae oriented vertically in the water column versus horizontally along the bottom. Taken together, these results suggest that *Macrocystis* collects large numbers of planktonic larvae from the middle and upper portions of the water column. Such larvae in the upper water column might otherwise pass above any shorter algae present in the absence of *Macrocystis* reducing settlement to a reef.

Macrocystis collects planktonic kelp bass because they have a strong affinity for algal structure. In the field, recently settled kelp bass were always closely associated with algal structure, tucked within the interstices formed by overlapping blades. In the lab, recently settled kelp bass spent a disproportionate amount of time near algae even though it occupied a small

proportion of the volume of the experimental tanks. In addition, this kelp bass affinity for algal structure increased both in the presence of predators and algal-associated food, experimental regimes more representative of natural conditions in the field.

The field and laboratory experiments revealed no evidence for preferential settlement to *Macrocystis* relative to other algae when volume and height in the water column were taken into account. However, kelp bass recruited in greater abundance to natural algal structure than to artificial structure of similar complexity, suggesting that algae in general might provide some sort of chemical cue or attractant, which does not appear to vary in strength among algal species. Field tests of algal selection as well as lab tests of algal preference provided no evidence of the ability of settlers to distinguish species of algae by chemical cues, and I know of no reports in the literature that fish are to particular algae based on chemical cues. However, given the potential effects of algae as refuge from predation (Ebeling and Laur 1985, Schmitt and Holbrook 1985, Holbrook and Schmitt 1988, Carr 1991b), as a source of associated food (see references in Carr 1991b), and given also the many invertebrate species that exhibit algal preferences based on chemical cues, the possible importance of such a mechanism warrants further investigation.

Others have proposed alternative mechanisms for increased recruitment of propagules in the presence of algal structure (reviewed in Carr 1991b). Two mechanisms of particular importance involve the effect of vertical structure on the direction and velocity of currents that carry propagules and the effect of algal structure on vulnerability of settlers to predators. First, my study did not address the effects of reduction of current velocities by *Macrocystis* and the

possible ensuing retention and accumulation of planktonic propagules, although this mechanism has been suggested for *Macrocystis* (Bernstein and Jung 1979, Jackson and Winant 1983, Jackson 1986) and a variety of short algae and macrophytes (Eckman 1983, 1987, 1990, Eckman et. al. 1989). Secondly, the role of macrophytes in reducing the vulnerability of fish to predation in the presence of plant structure has been indicated for freshwater plants (Savino and Stein 1982, 1989, Werner and Hall 1988), sea grasses (Orth et al. 1984), and marine algae (Ebeling and Laur 1985, Carr 1991b). With respect to kelp bass recruitment in particular, the presence of algal structure reduces vulnerability of settled kelp bass to predation and thereby enhances local recruitment (Carr 1991b). In addition, because predators are often most abundant near the bottom, the height of *Macrocystis* provides a spatial refuge in the upper water column (Carr 1991b). Predators also discourage the movement of settlers from their algal refuges, thereby reinforcing the initial patterns of settlement among algal species.

Enhanced recruitment in the presence of tall kelps appears to commonly occur in a wide variety of temperate reef fishes (Leaman 1976, Haldorson and Richards 1987, Larson and DeMartini 1984, Bodkin 1988, Carr 1989, 1991a 1991b). Importantly, all of these fish apparently recruit to the upper portions of these plants, suggesting that the mechanisms described here for promoting kelp bass recruitment to *Macrocystis* may generally apply to many other temperate reef fishes. Another important and common characteristic of this recruitment process is that almost all of these fish migrate down plants to the reef surface and gradually dissociate from the algae within the first year of life. This process

is also illustrated by the increase in recruitment to reefs caused by fish-aggregating devices (Beets 1989).

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Table 1. Mean percent cover of the five most abundant algae in areas without *Macrocytis* at Santa Catalina Island from 1985 to 1989. N = number of 30 m transects. Total is percent cover of the five most abundant species combined. S = *Sargassum*.

YEAR	ALGA (PERCENT COVER)				
	1985	1986	1987	1988	1989
N	56	53	44	25	15
<i>S. palmeri</i>	(36)	<i>S. palmeri</i> (34)	<i>S. palmeri</i> (40)	<i>S. palmeri</i> (64)	<i>S. palmeri</i> (56)
<i>Dicryptopteris</i>	(26)	<i>Dicryptopteris</i> (26)	<i>Zonaria</i> (24)	<i>Dicryptopteris</i> (15)	<i>Zonaria</i> (16)
<i>Zonaria</i>	(14)	<i>Zonaria</i> (24)	<i>Dicryptopteris</i> (19)	<i>Zonaria</i> (14)	<i>Dicryptopteris</i> (14)
<i>Colpomenia</i>	(9)	<i>S. muticum</i> (8)	<i>Halidrys</i> (3)	<i>Cystoseira</i> (5)	<i>Cystoseira</i> (6)
<i>Eisenia</i>	(4)	<i>Cystoseira</i> (3)	<i>Cystoseira</i> (2)	<i>S. muticum</i> (1)	coralline (4)
TOTAL	(89)	(95)	(88)	(99)	(96)

Table 2. Abundance of newly settled kelp bass among five algae at Santa Catalina Island. N = number of algal samples collected during the settlement period (August and September) from 1984 to 1988. Samples of all species except *Macrocystis* were collected in areas lacking *Macrocystis*. For all except *Macrocystis*, each sample (N) is an individual plant.

ALGA	N	TOTAL KELP BASS	TOTAL WEIGHT ALGAE (KG)	KELP BASS PER KG ALGAE
<i>Dictyopteris</i>	215	0	20.6	0
<i>Eisenia</i>	201	4	500.0	0.008
<i>Macrocystis</i>	15	277	198.7	1.34
<i>Sargassum</i>	635	3	128.2	0.023
<i>Zonaria</i>	238	1	16.5	0.06

Table 3. Recruitment of recently settled kelp bass to *Sargassum palmeri* suspended over six reef areas lacking *Macrocystis*. Values are summed across four collectors per site.

SITE	TOTAL KELP BASS	ALGAL WET WT. (KG)	KELP BASS PER KG ALGA
Bird Rock	14	4.9	2.9
Chalk Cove	27	5.0	5.4
Isthmus Reef (North)	13	5.5	2.4
Isthmus Reef (South)	10	5.2	1.9
Lion's Head	11	4.6	2.4
Ripper's	14	4.2	4.3

Table 4. Effect of height in the water column and algal type on recruitment of kelp bass.

ALGA DEPTH	ALGAE WT (KG)	ALGAE VOL (M ³)	TOTAL RECRUITS	PERCENT RECRUITS PER KG ALGAE	
				MEAN	(SE)
<i>Sargassum</i>					
Surface	7.6	0.61	61	26.5	(6.5)
Mid-depth	7.8	0.66	125	59.0	(4.2)
Bottom	6.1	0.70	11	14.5	(9.5)
<i>Eisenia</i>					
Surface	15.8	0.80	7	18.0	(2.0)
Mid-depth	15.1	0.75	44	54.0	(2.0)
Bottom	16.1	1.11	22	28.0	(4.0)

Two factor ANOVA:

SOURCE	DF	SS	F	P
ALGA	1	0.0005	0.05	0.838
DEPTH	2	0.3774	18.86	0.003
ALGA*DEPTH	2	0.0474	2.37	0.174

REGWF means comparison: Mid-depth > Surface = Bottom.

Table 5. Comparison of kelp bass recruitment to algae located horizontally along the bottom ("horizontal") and vertically up into the water column ("vertical"), and horizontally oriented algae.

A.

TRIAL	ORIENTATION	LOCATION	TOTAL ALGAL WEIGHT (KG)	TOTAL RECRUITS
1	Vertical	Inshore	9.5	39
		Offshore	9.1	56
	Horizontal	Inshore	10.0	13
		Offshore	8.7	19
2	Vertical	Inshore	13.6	57
		Offshore	12.9	64
	Horizontal	Inshore	13.4	21
		Offshore	12.2	24

B. Log Linear Analysis:

SOURCE	DF	Chi-Square	P
Orientation (O)	1	58.53	<0.0001
Location (L)	1	3.32	0.07
Trial (T)	1	5.09	0.02
O*L	1	0.00	0.95
O*T	1	0.14	0.71
L*T	1	0.82	0.37
O*L*T	1	0.00	1.00

Table 6. Algal selection by recently settled kelp bass during a 14 day exposure of algae to settlement in the field. Total values are summed across eight parcels of each natural and artificial alga at mid-depth and 1 m above the bottom (bottom depth = 8 m). Total recruits were compared among algal types with a chi-square analysis: number per 0.1 m³ algae ($\chi^2 = 8.85$, df=3, P = 0.01) and number per kg algae ($\chi^2 = 4.06$, df=3, P = 0.25).

ALGAL SPECIES	ALGAE		RECRUITS PER	
	VOL (m ³)	WT (kg)	VOL ALGAE (0.1 m ³)	WT ALGAE (kg)
<i>Macrocystis</i>	11.0	17.0	8.3	5.4
<i>Eisenia</i>	9.9	18.6	6.8	3.7
<i>Sargassum</i>	8.7	11.2	11.7	9.1
Artificial	8.4	3.7	1.3	3.0

Table 7. Effects of structural complexity (high vs low) and substrate type (natural vs artificial) on algal selection by kelp bass recruits.

STRUCTURAL COMPLEXITY	SUBSTRATE	ALGAL TYPE	N	RECRUITS PER DAY	
				MEAN (SE)	
High	Natural	<i>Sargassum</i>	10	3.6	(0.6)
High	Artificial	Plastic <i>Sarg.</i>	10	1.8	(0.3)
Low	Natural	<i>Macrocystis</i>	10	1.8	(0.3)
Low	Artificial	Plastic <i>Macro.</i>	10	0.8	(0.2)

THREE-FACTOR ANOVA RESULTS:

SOURCE	DF	SS	F	P
Substrate (S)	1	5.56	12.7	0.0019
Complexity (C)	1	5.53	12.6	0.002
Trial (T)	4	2.00	1.1	0.364
S*C	1	0.07	0.15	0.698
S*T	4	0.61	0.35	0.842
C*T	4	3.26	1.86	0.157
S*C*T	4	0.85	0.48	0.748

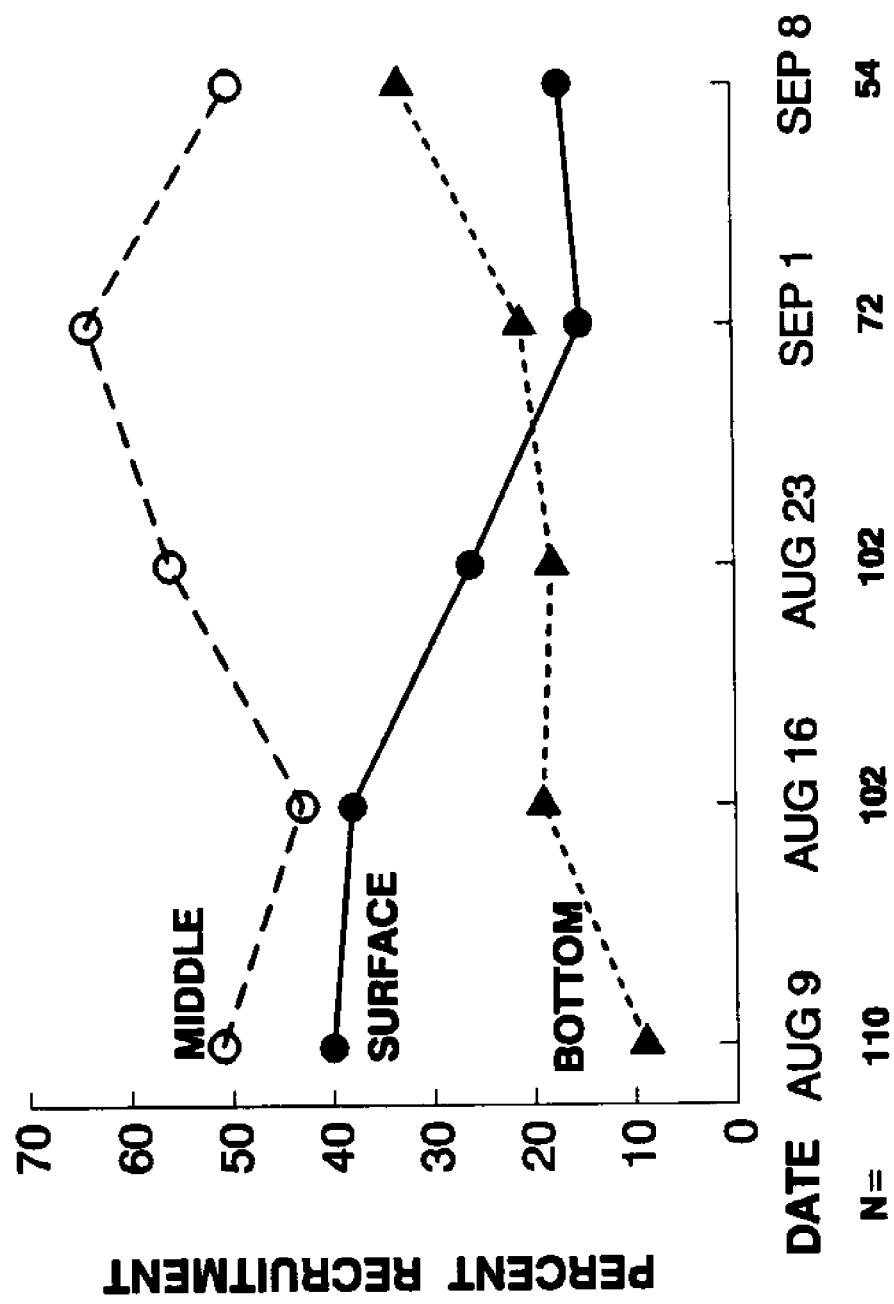
FIGURES

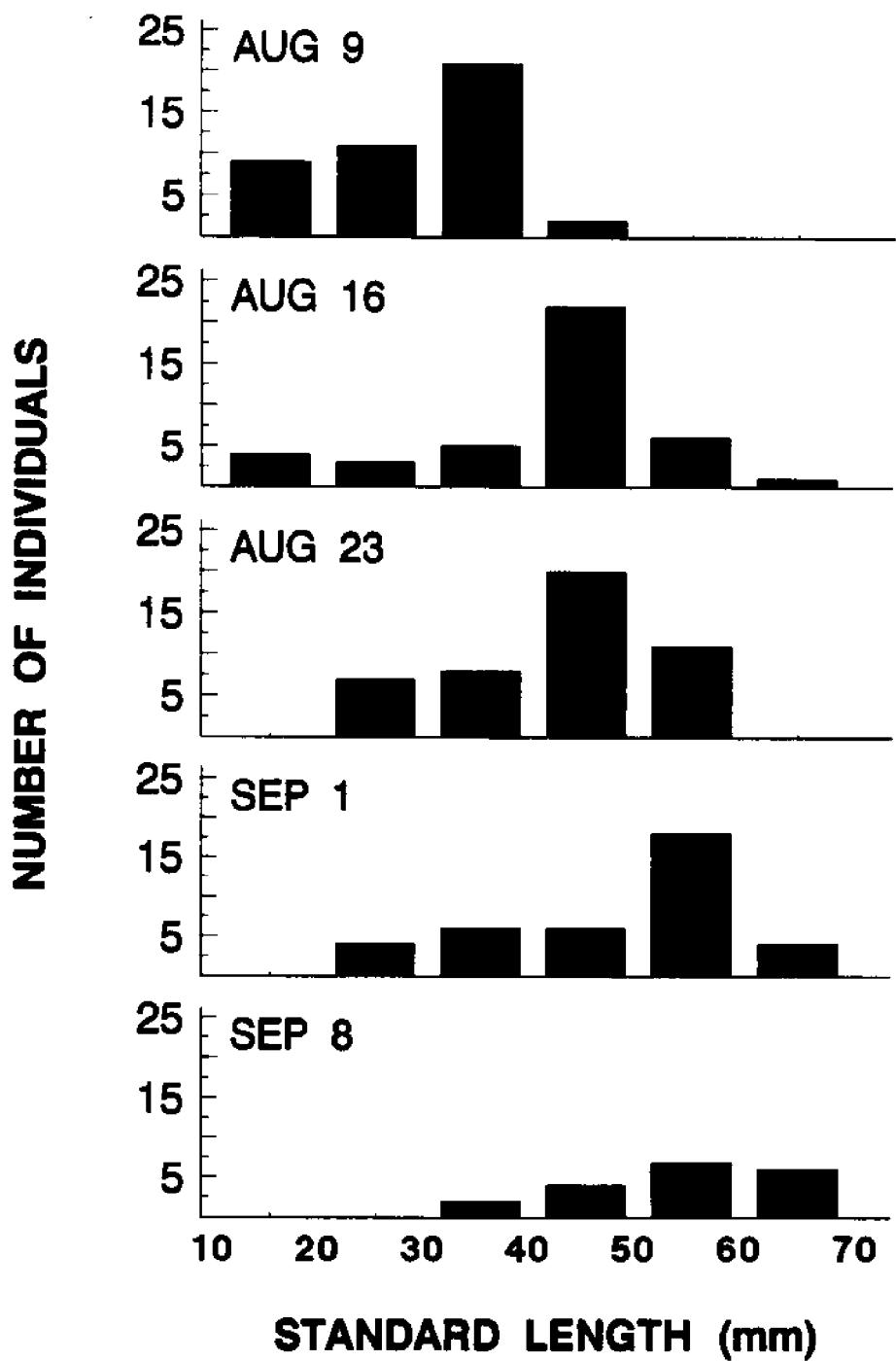
Figure 1. Relative abundance of a cohort of kelp bass recruits over time within the upper, middle and bottom third of *Macrocystis* plants. Plotted is the percent of total recruits summed across 18 *Macrocystis* plants per sampling date. N is the total number of recruits per sampling date.

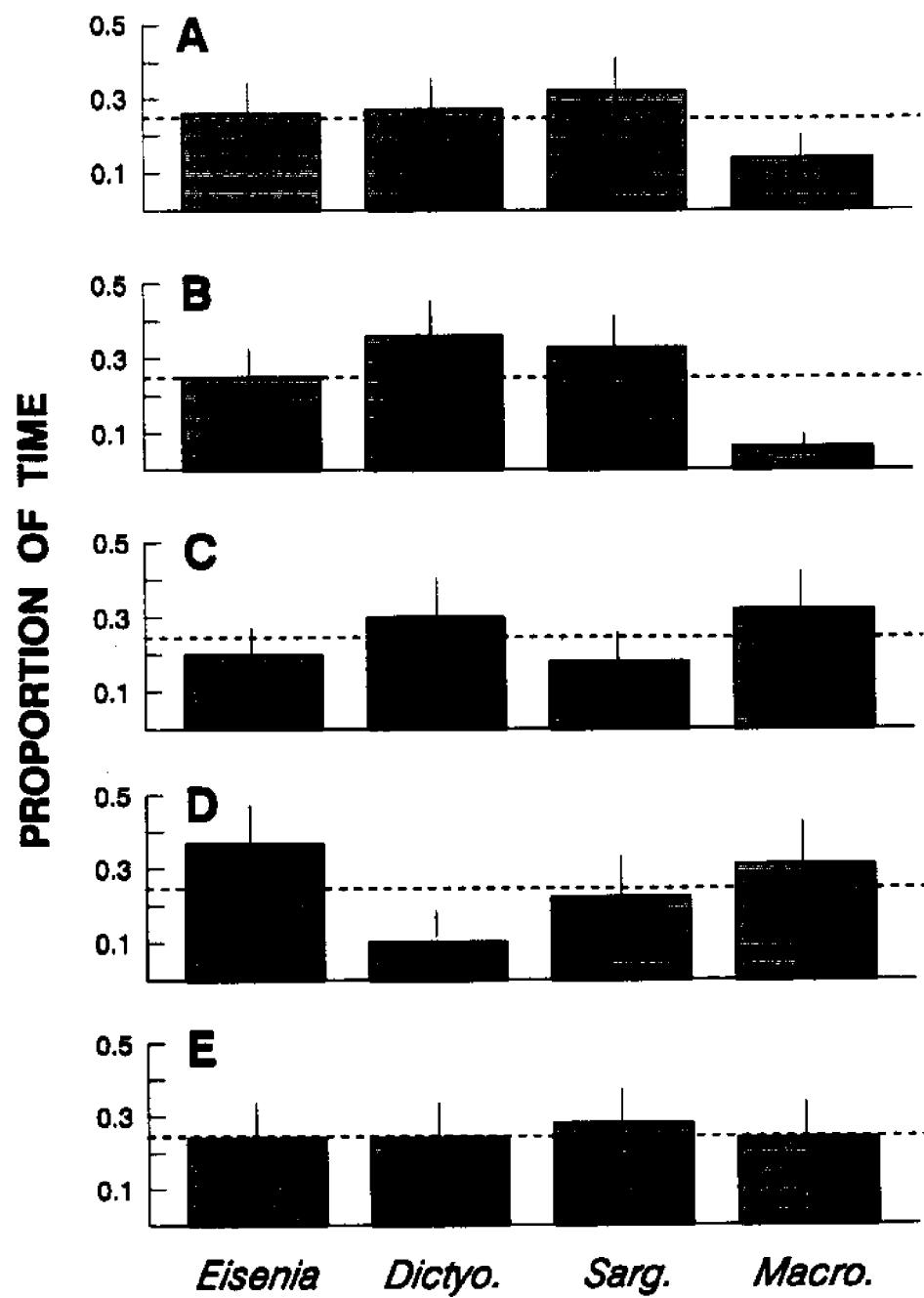
Figure 2. Percentage of kelp bass recruits within size categories on *Macrocystis* plants censused for vertical distribution of recruitment (Figure 1).

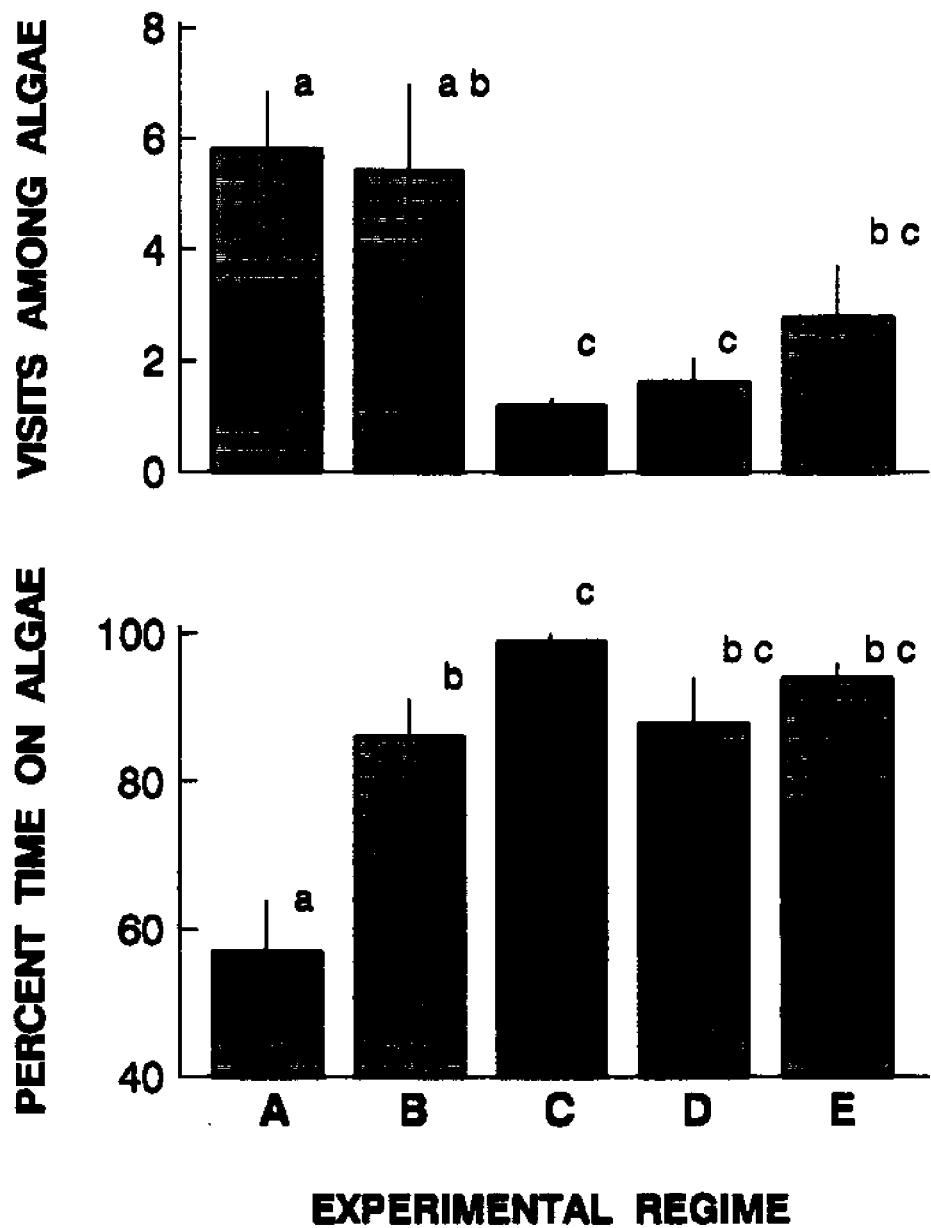
Figure 3. Preference for algal species by recently settled kelp bass in laboratory choice experiments. Preference was measured as the proportion of time spent with each algal species over a 20 min trial. Regimes of preference tests include fed vs starved fish (A vs B), predators absent vs present (A vs C), midday vs dusk (C vs D), and food absent vs present on algae (B vs E). All other factors (time of day, predator presence, food presence, and state of hunger) were the same for each pairwise comparison. Dashed horizontal lines are expected proportion of time given no preference (0.25). Number of individuals (trials) tested under conditions A, B, C, D, and E was 16, 16, 22, 18, and 18, respectively.

Figure 4. Effect of five experimental conditions on movement and affinity for algal structure by recently settled kelp bass. Movement was measured as the number of visits among algal clumps during a 20 min trial. Algal affinity was measured as the percent time spent within 5 cm of algal structure, all species combined. Conditions A through E correspond to those described for Figure 3 (see legend). Values plotted are means \pm 1 SE.









CHAPTER 3

EFFECTS OF PREDATORS ON RECRUITMENT AND HABITAT USE BY A TEMPERATE REEF FISH

INTRODUCTION

Reef fish populations are commonly established and maintained by the recruitment of planktonically dispersed larvae or juveniles (see reviews by Sale 1980, Richards and Lindeman 1987, Doherty and Williams 1988, Mapstone and Fowler 1988). An understanding of the dynamics of such fish populations requires knowledge of the recruitment process, particularly of mechanisms responsible for spatial and temporal variation in recruitment. Mechanisms contributing to patterns of recruitment (*sensu* Keough and Downes 1982, Connell 1985) of planktonically dispersed larvae involve factors influencing larval production, supply, settlement, and post-settlement survival and movement. Whereas much attention has focused on the variable supply of larval fishes among sites (Sale 1980, Williams 1980, Doherty 1983, Victor 1983, 1986, Doherty and Williams 1988, Mapstone and Fowler 1988), processes occurring during settlement and postsettlement periods also effect patterns of recruitment. Of these processes, the role of predators as determinants of spatial and temporal variation in recruitment has been largely neglected. Such neglect is surprising given the extent of theoretical and empirical evidence for the importance of predation to population structure and dynamics in aquatic systems (Kerfoot and Sih 1987).

Two lines of evidence have been pursued to assess the importance of predation to spatial and temporal patterns of reef-associated fish recruitment (see review by Hixon *in press*). The first includes correlative relationships between recruitment and intensity of predation (Shulman et al. 1983, Thresher 1983, Hixon and Beets 1989). The second involves measuring the response of

recruitment to experimental manipulation of the intensity of predation (Thresher 1983, Shulman 1984, 1985, Doherty and Sale 1986, Behrends 1987, Hixon and Beets 1989). In both cases, the intensity of predation is estimated either directly, by variation in the abundance of predators (Thresher 1983, Shulman et al. 1983, Shulman 1985, Doherty and Sale 1986, Hixon and Beets 1989), or indirectly, by variation in the availability of shelter for prey (Shulman 1984, 1985, Hixon and Beets 1989) or both (Behrends 1987).

The preferred method of assessment of the effects of predation on recruitment is the experimental manipulation of predator abundance. Though correlative evidence provided by natural variation in predator abundance and recruitment suggests the effects of predation, experiments are required to establish the causal effect of predators. Since the amount of available refuge (e.g., provided by structural complexity) may covary with the abundance or productivity of prey and with other influences of habitat complexity, the effect of refuge on predation is not easily isolated. Consequently, refuge manipulations involve inherent difficulties of interpretation.

Algae provide an extremely important source of structural complexity to shallow temperate marine reefs. Although such structure has long been argued to provide an important refuge for fishes, little direct experimental evidence has been presented for temperate marine species. Manipulations of the presence of predators has been shown to influence the distribution of juvenile surfperches among algal species (Schmitt and Holbrook 1988). Likewise, reductions, relative to controls, in the density of juvenile surfperch after experimental removal of the kelp *Pterygophora californica* were attributed to a redistribution of juvenile surfperch to sites with intact algal structure (Ebeling and Laur 1985).

However the effect of predators on the local magnitude of recruitment or differential recruitment among algal habitats has not been demonstrated. The presence of algae has been shown to influence patterns of recruitment of planktonically dispersed temperate marine fishes (Jones 1984, Larson and DeMartini 1984, Haldorson and Richards 1987, Carr 1989, 1991a, 1991b, Love et al. 1991). Further, the spatial and temporal occurrence of algal assemblages on temperate reefs are highly dynamic (Dayton 1985, Schiel and Foster 1986). Consequently algal dynamics can be an important source of spatial and temporal variation in the density of recruits of some species (Carr 1991a). The extent to which predation contributes to this relationship is not known.

This study investigates the effect of predation on the recruitment of a planktonically dispersed temperate reef fish, the kelp bass (*Paralabrax clathratus*). Planktonic larvae settle on shallow rocky reefs where they eventually contribute to local reef-associated populations. Previous studies indicate that local recruitment is enhanced by the presence of the giant kelp, *Macrocystis pyrifera* (Larson and DeMartini 1984, Carr 1989, 1991a, Holbrook et al. 1990). Here, I examine whether differential predation can influence local recruitment and differences in recruit density among algal habitats. In this study I estimate the relative abundance of predators in each habitat type, the vulnerability of young bass to the predominant predators in each habitat, and the behavioral responses (habitat use) of young kelp bass in the presence and absence of predators.

METHODS**Study Area**

All field and laboratory experiments were conducted at the Catalina Marine Science Center, University of Southern California, located along the northwest coast of Santa Catalina Island ($33^{\circ}27'N$: $118^{\circ}29'W$). Santa Catalina Island lies 40 kilometers offshore of Los Angeles, California. Post-larval kelp bass recruit to shallow (≤ 10 m) rocky reefs which vary widely in rock relief (0-3 m) and density of giant kelp, *Macrocystis pyrifera*, plants (0-450 fronds $\times 30\text{ m}^{-2}$). The relative abundance of *Macrocystis pyrifera* (hereafter *Macrocystis*) and the dominant understory alga, *Sargassum palmeri* (hereafter *Sargassum*), varies widely among reefs.

I. Effect of predation on the magnitude of local recruitment.

To determine if predators can affect the magnitude of kelp bass recruitment, and if predation contributes to the generally lower recruitment of kelp bass to reefs lacking *Macrocystis* (Carr 1989, 1991a), I compared recruitment of kelp bass among reefs on which I manipulated predator presence. Reefs lacking *Macrocystis* were simulated by constructing isolated 1 m^2 plots of *Sargassum* attached to rocks, with similar bottom depth (range = 7.6 to 9.1 m), rock relief (10 rocks per reef), and biomass and percent cover of *Sargassum* (range = 80-100%). Sampling of nearby reefs indicated that *Sargassum* was the predominant algal species, constituting 61% of the total algal

biomass on shallow reefs, and weighed $1.3 \pm 0.3 \text{ kg m}^{-2}$ ($n = 32$ random 1 m^2 quadrats). Therefore to approximate natural total algal biomass (all species combined), experimental reefs of 100% *Sargassum* should approximate $1.3/0.61 = 2.1 \text{ kg m}^{-2}$. The mean (± 1 std. dev.) biomass of *Sargassum* added to each reef was $2.7 \pm 0.06 \text{ kg m}^{-2}$. Reefs were constructed on a featureless sand substratum and were separated by 6-7 m of sand to inhibit post-settlement movement of recruits between reefs.

Three treatments were randomly allocated among the fifteen reefs. The predator exclusion treatment consisted of reefs built within 1 m^3 cages constructed of 2 cm dia pvc pipe covered with $5 \times 5 \text{ mm}$ sq nylon mesh netting. This mesh dimension allowed newly settling larvae to pass into the cage but prevented larger predators from foraging over the reef. Cages were enclosed on all sides (including the bottom); a hinged top provided access at the end of the experiment (Figure 1a). The top was secured during the 2 wk duration of each trial. Cage controls ($n = 5$ reefs) were constructed of the same material with netting only on the top and upper half of the four sides (Figure 1b), permitting predators to forage on the reef. The remaining five reefs were left uncaged (Figure 1c). Each of the fifteen reefs were constructed upon an open flattened bag of $1 \times 1 \text{ mm}$ sq mesh material. The walls of the bag were secured flush with the substratum around the circumference of the reef. To sample fish on a reef at the end of the two week period of an experiment, the walls of the bag were raised around the reef and all rocks and all but two plants were removed from the bag. Fish were shaken from plants prior to removal from the bag. After removal of all but two plants (upon which fish aggregated), the mouth of the bag was secured and fish were collected and counted in the lab.

The experiment was conducted twice, each trial lasting for a two-week period (July 31 to August 15 and August 16 to 29). Treatments were randomly allocated to the reefs in each trial. Two hypotheses were tested: (1) there are no cage effects, by testing the difference between mean number of recruits per reef ($n=5$) on the predator-accessible (no cage) and cage-control (half-cage) treatments, and (2) there is no predator effect, by testing the difference between the predator-exclusion (full cage) and predator-accessible (half-cage and no-cage) treatments.

A pilot study was conducted during 1988 to assess predator use of the uncaged and half-caged treatments. Reefs were visited on separate days and all predators (primarily older juvenile kelp bass) within 1 m of each reef were counted. Predator abundance per reef was compared for each trial separately over time (day) and among treatments (cage) using repeated measures ANOVA.

II. Predation risk of young-of-year kelp bass among algal habitats.

This experiment was designed to test for differences in the vulnerability of young-of-year kelp bass among three habitats, i.e., the *Macrocystis* canopy ("upper kelp"), the lower portions of *Macrocystis* plants ("lower kelp"), and the *Sargassum* habitat. *Sargassum* is the dominant alga on reefs devoid of *Macrocystis* at this site. Vulnerability of young bass per predator was estimated for each of the three algal habitats by simulating the three algal habitats in 600 l (1 m X 2.5 m dia) aquaria (one habitat per aquarium) and measuring predation rates (proportion of prey fish eaten per 24 hr period) by a standardized number

of predators. A structure-free (i.e., algal-free) control was also conducted to assess if predators were inhibited from feeding under the experimental conditions.

The upper portion of *Macrocystis* was simulated in the experimental tank by suspending 4 bundles of *Macrocystis* fronds collected from the uppermost 1 m of *Macrocystis* plants. Each bundle was anchored to the bottom of the tank and consisted of 7 fronds, each 2 m long, forming a canopy of fronds at the surface characteristic of natural *Macrocystis* canopies. The bottom portion of *Macrocystis* plants was simulated by transplanting the bottom 1 m of four *Macrocystis* plants (rock, holdfast and fronds) into the experimental tank. The *Sargassum* habitat was simulated by transplanting several *Sargassum* plants attached to rocks into the experimental tanks. All plant sizes and densities used in the experimental tanks approximate mean values of each species in the field. Ambient densities of prey associated with each alga were transplanted with the algae by collecting each alga in 0.33 mm² mesh Nitex bags. Simulated algal habitats were supplemented with prey by occasionally replacing plant material between trials. Ambient light conditions in each of the three habitat types and the algal-free environment were measured in the field with an irradiance meter (Biospherical Instruments digital scaler) with a spherical (4 phi) collector. Light levels characteristic of each habitat were simulated in the experimental tanks by covering tanks with plastic sheeting of varying opaqueness (Table 1).

Young-of-year kelp bass of three size classes (15-30 mm, 35-45 mm and 68-78 mm standard length (SL: base of tail to anterior end) corresponding approximately to ages 1, 2, and 11 mo, respectively, were tested separately. The initial densities of prey fish of each size class used in the experiments (40, 20

and 8 per 19.6 m³, respectively) are densities which I frequently encountered in the field. Kelp bass were maintained in aquaria prior to a trial and added to the experimental tank 10 min before the release of predators. To facilitate collection of the prey fish at the end of the experiment, the bottom and walls of each tank were lined with 1 mm² mesh netting, sewn and weighted to conform to the sides of the tank. At the end of the 24 hr trial, algal structure was cleared from the tank and examined carefully for prey fish. The mesh liner was then lifted to the surface of the tank, collecting all remaining prey fish which were removed and counted. Prey fish were used only once in each habitat/predator combination.

Predation rates by two predator species were estimated separately in each habitat type. Adult giant kelp fish, *Heterostichus rostratus*, ranging in size from 200 to 270 mm SL were tested in pairs and only with the smallest kelp bass (15-30 mm) as prey. Older (ca. 24 to 36 mo) kelp bass, *Paralabrax clathratus*, from 135 to 195 mm SL were tested in groups of three. Each predator group was used only once for each habitat type. Predators were maintained in aquaria on minced frozen squid and starved 24 hr prior to each trial. Predators were placed in a 2 cm² vexar mesh tube (70 X 40 cm dia) within the experimental tank for a 10-30 min period prior to release into the tank. This period presumably allowed prey and predators to adjust to the presence of one another and to the algal habitat prior to any foraging attempts.

Effects of algal habitat and young-of-year bass size on percent mortality were assessed using a two-factor ANOVA and an a posteriori means comparison (Ryan-Einot-Gabriel-Welsch Multiple F, hereafter REGWF).

Proportions were arcsin(square root) transformed for analysis.

III. Relative abundance of predators among algal habitats.

To determine if the abundance of predators differed among the upper *Macrocystis*, lower *Macrocystis* and *Sargassum* habitats, their species composition and density was estimated in each algal habitat. Predator density was estimated by visual counts of each species (by size class) encountered along 1 X 2 X 30 m transects in each of the three habitat types on several reefs ($n = 26, 26$, and 30 transects in the upper *Macrocystis*, lower *Macrocystis* and *Sargassum* habitats, respectively). Predators were recorded by species and size class. Only fish ≥ 5 cm total length were counted for each predator species. Sampling was conducted within the three month (August-October) settlement period of kelp bass during 1988. The most abundant and ubiquitous predators, older kelp bass, were sampled again in October of 1989 ($n = 102, 102$ and 35 in the upper *Macrocystis*, lower *Macrocystis*, and *Sargassum* habitats, respectively). The mean densities of older kelp bass, and of all predator species combined, were compared among the three habitat types using a single factor ANOVA and the REGWF *a posteriori* means comparison.

IV. Behavioral response of young-of-year kelp bass to the presence of predators.

To determine the behavioral response of young-of-year kelp bass to the presence and absence of predators (24 to 36 mo old kelp bass), I measured

three response variables: their habitat use (i.e., distribution among *Sargassum*, *Macrocystis*, the water column, and open sand bottom), their proximity to algal structure, and their feeding rate in each habitat. Predator exclusion was achieved with a 6 m tall by 9 m dia exclosure of 5 mm mesh Atlas netting. The exclosure covered 50 m² of bottom; it was placed over sand bottom, and algae-covered rocks were transplanted into the exclosure. The exclosure was partitioned in half (25 m² each) with a 6 m by 9 m wall of 3 mm mesh Atlas netting. One (ca. 7 m tall by 0.5 m dia) 30 frond *Macrocystis* plant and a 3.3 m dia patch of *Sargassum* (attached to rocks) were transplanted into each side of the exclosure. Surface area of the *Macrocystis* plant, *Sargassum* patch and open sand substratum were approximately 11 m², 10.5 m² and 13 m², respectively.

Two experiments were conducted, the first (September 1988) using young bass of a size (30-40 mm SL) which allowed individual tagging for mortality estimates, and the second (August 1989) in which young bass recruited from the plankton. The first experiment consisted of six "trials" constituting temporal replicates. Each trial involved adding approximately 25 young-of-year kelp bass (30-40 mm SL) to each side of the exclosure and seven 1-2 year old kelp bass to one side only. To estimate an appropriate density of predators to include in the exclosure, a similar sized area (25 m²) of *Sargassum* reef and a *Macrocystis* plant were established outside and nearby the net exclosure. Predator abundance was recorded three times a day (dawn, midday, and dusk) on 16 days over a 3.5 week period. Mean abundance (\pm 1 std. error) of \geq 1 yr old kelp bass in this area was 7.4 (\pm 1.0). Predators were added one day earlier than young-of-year and I began making observations one day after addition of the young-of-year. Observations of young-of-year feeding rate (bites per

individual per 4 min period), proximity to algal structure (0 m, 0-0.3 m, >0.3 m), and number associated with each habitat type (*Macrocystis*, *Sargassum* reef and open sand bottom) were recorded three times daily (dawn, midday and dusk) for three consecutive days per trial. Additionally, the distribution of predators among habitat types was recorded. At the end of each trial, all young-of-year were collected from the exclosure and predators were transferred from one side of the partition to the other for the next trial. A new set of young-of-year were used for each trial.

The effect of predators on the feeding rate of young-of-year kelp bass was assessed by comparing feeding rates (no. of bites per individual per 4 min period) of fish in the presence and absence of predators. Because predators were found to influence the distribution of young-of-year bass among algal types, the effect of algal type (*Sargassum*, *Macrocystis*) on feeding rate was also estimated. Predator and algal effects were assessed simultaneously to determine if either of these two variables influenced the effect of the other on feeding rates of the young bass.

Predator (presence/absence) effects on the distribution of young-of-year were analyzed using a two factor MANOVA (Hotelling-Lawley Trace). Young-of-year distribution was described as the array of proportions of individuals among proximity categories and among habitat types. The effects of predator (presence/absence) and algal type (*Sargassum*, *Macrocystis*) on feeding rate of young-of-year kelp bass were tested with a two factor ANOVA.

The second experiment examined the effect of predator presence on fish which had recruited directly from the plankton into the exclosure. The design was similar to the first experiment; however, planktonic kelp bass that recruited

through the mesh of the net enclosure were allowed to accumulate over a 33 day period prior to sampling their distribution (August 3 to September 5). The important differences between this experiment and the first are that (1) young kelp bass were of smaller average size (recruits settle at 10 mm SL), and (2) density of the young bass was not controlled between the two predator levels. This experiment included only one trial. Young-of-year bass were counted and recorded by habitat type eight times over a three day period.

RESULTS

I. Effect of predation on the local density of recruits.

Predation strongly affected the local recruitment of kelp bass. In both trials, recruitment to areas where predators were excluded was significantly greater than to the two treatments which included predators (Trial 1: $F = 60.31$, $df = 1,12$, $P = 0.0001$; Trial 2: $F = 11.3$, $df = 1,12$, $P = 0.006$; Figure 2). Recruitment to the cage-control and predator-accessible (no cage) treatments was not significantly different, suggesting a lack of cage effects (Trial 1: $F = 3.58$, $df = 1,12$, $P = 0.08$; Trial 2: $F = 3.22$, $df = 1,12$, $P = 0.10$; Figure 2).

Predator abundance at the cage-control and predator-accessible treatments did not differ significantly during the 1988 pilot study and trial 1 of 1989, but was significantly greater at the cage control during the second trial of 1989 (Table 2). This pattern suggests that predator occurrence in uncaged and cage control (half-cage) treatments was generally similar and that similar

recruitment of kelp bass to these treatments reflected similar intensities of settlement and predation rates (i.e., no cage effect on the magnitude of settlement).

II. Vulnerability of young kelp bass in different algal habitats.

Vulnerability of young-of-year kelp bass, measured as the percent mortality of young-of-year during the 24 hr exposure to predators (older kelp bass) in experimental tanks, was strongly affected by the presence of algal structure and prey size, but did not differ among algal habitats (Figure 3, Table 3). Small young-of-year bass suffered greater mortality than large individuals in all habitat types, and the difference was greatest in the structureless (no-algae) control where predation rate was significantly different among all three size classes. Thus, the presence of algae resulted in significantly decreased predation by older kelp bass on the small and intermediate sized young-of-year, but did not influence predation on the largest size class. This suggests that refuge provided by algal structure is of decreasing importance for larger sized fish. Furthermore, since each of the three algal habitats provided similar protection from predation, vulnerability in the field is more likely a function of the relative abundance of older kelp bass among habitats rather than differences in algal structure.

With respect to the second most ubiquitous predator, the giant kelpfish, *Heterostichus rostratus*, vulnerability of the smallest size class (15-30 mm) of young-of year kelp bass also declined significantly in the presence of algal structure but did not differ significantly among algal habitats (Table 4). This

pattern of habitat-specific vulnerability to predation by giant kelpfish is similar to the pattern of vulnerability to predation by older kelp bass.

III. Relative abundance of predators in different algal habitats.

I recorded 8 species of piscivorous fishes within the three algal habitats in the field. These included (in descending order of abundance) older kelp bass (*Paralabrax clathratus*), island kelpfish (*Alloclinus holderi*), giant kelpfish (*Heterostichus rostratus*), spotted kelpfish (*Gibbonsia elegans*), scorpion fish (*Scorpaena guttata*), treefish (*Sebastes serriceps*), and the kelp and grass rockfishes (*S. atrovirens* and *S. rastrelliger*, respectively) (Table 5).

Overall predator density (all species combined) differed significantly among habitats, declining in order from the lower *Macrocystis*, open bottom, and upper *Macrocystis* habitats, respectively (Table 5; Single-factor ANOVA and REGWF means comparison: $F = 15.5$, $df = 2,80$, $P = 0.0001$). All eight species occurred in the lower *Macrocystis* and open bottom habitats, whereas only two of these species (giant kelpfish and older kelp bass) were encountered in the upper *Macrocystis* habitat. This pattern of predator abundance between habitats was strongly influenced by the most abundant and ubiquitous predator, older (primarily 1 and 2 yr) kelp bass (Table 5 and Table 6).

IV. Behavioral response of young-of-year kelp bass to the presence of predators.

The distribution of larger young-of-year kelp bass across algal habitats

was strongly influenced by the presence of predators (older kelp bass) (MANOVA: $df = 2,19$, $F = 13.66$, $P = 0.0002$). In the presence of predators, the majority of 30-40 mm young bass were closely associated with the understory alga, *Sargassum*; fewer fish occurred on giant kelp and the sand (Figure 4). In the absence of predators, young kelp bass were more evenly distributed among algal habitats. Therefore the effect of predators was to restrict habitat use by the young-of-year bass. It is important to note that these shifts in habitat use did not reflect differences in density of young bass due to differential recruitment or mortality, as these two factors were controlled by adding equal numbers and recording only tagged individuals in the experiment. Consequently, changes in habitat use reflect behavioral responses of the young bass to the presence of predators. The distribution of young bass was not affected by time of day (morning, mid-day, and evening) (MANOVA: $df = 2,19$, $F = 0.68$, $P = 0.52$) nor was the predator effect influenced by time of day (i.e., no time by predator interaction; MANOVA: $df = 2,19$, $F = 0.19$, $P = 0.83$). There was no detectable effect of predators on the feeding rate of young bass in this experiment (Table 7). Nor was there a significant difference in feeding rate between fish inhabiting the two algae (*Macrocystis* and *Sargassum*).

The presence of predators also influenced the among-habitat distribution of recruited young-of-year bass examined in the second experiment. Again the effect of predators was to restrict habitat use by young bass; however, the direction of the effect (Table 8) was the opposite of that exhibited by the larger young-of-year bass. In the presence of predators, few fish occupied open habitats (i.e., open water column or sand) and the majority (74%) of individuals occurred close (<0.3 m) to *Macrocystis* rather than *Sargassum*. In the absence

of predators, young bass were more equally distributed among the *Macrocystis*, *Sargassum* and open habitats (Table 8). However in this experiment final density of young bass differed approximately two-fold between treatments (48 in the predator inclusion and 101 in the predator exclusion) as determined by collection of all individuals from the exclosure at the end of the trial. Consequently, the relative effect of predator level and young bass density on habitat use of the young bass can not be determined.

DISCUSSION

Recently, frequent (i.e., daily) sampling of recruitment between separate but similar habitats has led to an emphasis on the importance of variable larval supply to patterns of recruitment (see reviews by Doherty and Williams 1988, Mapstone and Fowler 1988). Such variable recruitment resulting from spatial and temporal variation in larval supply has been referred to as "recruitment limitation" (*sensu* Doherty 1983) or "recruitment regulation" (*sensu* Hughes 1990). However, rarely is recruitment monitored frequently enough to measure larval supply. And in fewer cases can monitoring of recruitment distinguish between larval supply and habitat preferences by settling larvae. Consequently, measures of recruitment often reflect influences of pre-settlement, settlement (Sweatman 1983, 1985) and post-settlement (Shulman 1984, 1985, Shulman et al. 1983) factors that contribute to mortality and movement of potential recruits. Further, variable post-recruitment growth (Doherty 1983, Victor 1986, Jones 1987, 1990, Forrester 1990), mortality (Shulman and Ogden 1987) and

movement (Robertson 1988) may obscure patterns of distribution and abundance initially established during recruitment.

This study supports the hypothesis that predation influences local fish recruitment. In particular, predation probably contributes to the differences in recruitment of recently settled kelp bass between algal habitats. These conclusions are based on the combined results of experimental manipulations (predator effect on local density of recruits and vulnerability of recruits in different algal habitats) and correlative evidence (predator abundance and distribution of recruits across algal habitats). Predator effects on recruitment were demonstrated in isolated manipulations of predators in the algal habitat to which recruitment is generally lowest (Carr 1989, 1991a): reefs covered with *Sargassum* in the absence of *Macrocystis*. Differences in vulnerability of recently settled kelp bass among the three algal habitats were not detected by the laboratory experiments. This suggests that the predator effect demonstrated in the *Sargassum*-dominated understory is similar in all three algal habitats, depending on the relative abundance of predators. The highest density of recently settled kelp bass (Carr 1991a) is associated with the lowest density of predators in the upper portions of *Macrocystis* (Table 5).

Previous studies of the effects of predators on the recruitment of temperate marine reef fishes have demonstrated distributional (Ebeling and Laur 1985, Schmitt and Holbrook 1985, Holbrook and Schmitt 1988a) and foraging responses (Holbrook and Schmitt 1988b) of young-of-year recruits to the presence of predators. In these studies, the response of young fish was to move to algal habitats that afforded greater protection from predation. While such studies demonstrate the importance of algal structure as refuge for young

fishes and the indirect effects of predation on habitat use, they offer only circumstantial evidence for the effect of predators on the local density of recruits. The results of this study provide evidence that predators can influence the local density of recruits of a temperate reef fish. Two important implications for patterns of local population replenishment by larval recruits arise from these results: (1) spatial and temporal patterns of predator abundance can strongly influence patterns of larval recruitment, and (2) spatial and temporal variation of algal abundance may contribute as well.

Manipulations of algae (presence/absence) have demonstrated a causal effect of algae on the distribution and abundance of temperate reef fish recruitment (Jones 1984, Ebeling and Laur 1985, Carr 1989, 1991a, 1991b, Schmitt and Holbrook 1990). Further, differences between species in the effect of algae on recruitment have also been demonstrated for assemblages of reef fishes in southern (Carr 1989) and central (Carr 1991b) California. Together, these results suggest that the effect of algae on reef fish recruitment may influence the species composition (i.e., relative abundance of species) of a reef-associated assemblage.

It is particularly important that the most abundant and ubiquitous predator of young-of-year kelp bass appears to be older kelp bass. Cannibalism is thought to be a potentially important determinant of cohort strength and the population dynamics of a wide variety of organisms including fishes (see reviews by Fox 1975, Polis 1981, 1984, and Dominey and Blumer 1984). Cannibalism can strongly influence size structure of a cohort (DeAngelis et al. 1979) as well as year class strength (Alm 1952, Chevalier 1973, Forney 1974, 1976). Such effects may be manifested even when the prey comprise a very small fraction of

the total diet of individual predators. Le Cren (1965) and Chevalier (1973) both demonstrated that low contributions of cannibalism to a predator's diet (1 and 3 percent, respectively) can account for 88-100% mortality of a year class of two freshwater fishes. This is particularly important in long-lived species, like kelp bass, in which numbers of older individuals accumulate over several year classes.

Cannibalism has only recently been shown to influence habitat use by young fishes (Schlosser 1987, Foster et al. 1988) and to induce differential habitat use among juvenile and adult conspecifics. In my study, the effect of predators was to reduce the breadth of habitat types used by young kelp bass. In the presence of predators, recently settled and older recruits used one algal habitat predominantly (*Macrocystis* and *Sargassum*, respectively), whereas in the absence of predators young fish not only used both algal habitats but also occurred in areas void of algae. The consequences of such increased habitat breadth are contingent on the relative rewards (particularly foraging rewards) in different habitats. Differences in foraging rates of young kelp bass between the two algal habitats were not detected. Consequently, if foraging success is density dependent (due to intraspecific competition or interference), increased habitat breadth may increase individual foraging success as well as allow fish to forage on a broader array of prey types (substrate-oriented prey as well as plankton). Such indirect effects of predators on prey growth rates have been demonstrated for young-of-year freshwater fishes (Mittelbach 1986, 1988, Mittelbach and Chesson 1987).

Predators may also contribute to habitat shifts exhibited by young-of-year kelp bass. Young bass that settle on *Macrocystis* plants eventually move down

onto the adjacent understory algae within a few months. Mean size of individuals during this habitat shift is 35 mm SL (Carr 1991a). In the presence of predators, both naturally and in the field test of habitat use, the majority of fish smaller than 35 mm SL inhabit *Macrocystis*. In contrast, fish greater than 35 mm SL, which exhibit the shift from *Macrocystis* to *Sargassum* naturally, occurred predominantly in *Sargassum* in the presence of predators in the field experiment. Therefore, predators in the lower portion of the water column may initially reduce recruitment of kelp bass there, thereby restricting recruitment to the upper portions of *Macrocystis*. Later, predators may somehow promote movement of larger (≥ 35 mm SL) young-of-year to the adjacent understory habitat. Although the laboratory studies indicate that larger young-of-year are less vulnerable to predation, these tests did not detect differences in vulnerability between algal habitats. Perhaps the laboratory experiments may have not detected a lower vulnerability to predation in *Sargassum* for these larger fish as suggested by the behavioral shift observed in the field experiment. An alternative explanation is that foraging success is greater in the *Sargassum* habitat for fish greater than 35 mm SL. Size-related shifts to habitats of greater foraging profitability by individuals of reduced vulnerability has been described in other systems (Werner et al. 1983, Mittelbach 1984, Werner and Gilliam 1984, Foster et al. 1988).

These effects of cannibalism (year class strength and habitat use) imply a potentially important compensatory mechanism for local populations of kelp bass. Reduced abundance of adults may alleviate predation rates of potential recruits, whose increased survival compensates for increased adult mortality. Furthermore, broader habitat use by young kelp bass in the absence of adults

suggests that foraging success may be influenced by local adult abundance. The ability of fish to forage among a wider array of habitat types may enhance foraging success and growth, depending on the relative rewards (i.e., foraging success) provided by different algal habitats (Holbrook and Schmitt 1984, 1988a, 1988b, Schmitt and Holbrook 1985). Consequently, reductions in adult numbers may enhance growth of young-of-year during a period of high vulnerability to predation. Vulnerability of kelp bass to predation is strongly size-dependent, as demonstrated in the mortality experiments presented here. Therefore, enhanced growth probably translates into increased survivorship of a cohort as well. Experimental demonstration of such effects of adults on young-of-year growth performance would provide valuable insight as to the mechanisms determining year class strength of this species.

The predator effects described here possibly influence larger scale patterns of recruitment since the three algal habitats examined in this study constitute major algal habitats characteristic of shallow reefs throughout the range of this species. The spatial and temporal occurrence of giant kelp, *Macrocystis pyrifera*, is highly dynamic (see reviews by Dayton et al. 1984, Dayton 1985, Schiel and Foster 1986) suggesting that the refuge from predation provided by this alga is spatially and temporally variable as well. Annual variation in the presence and abundance of giant kelp does contribute to annual variation in the strength of local recruitment (Carr 1991a). Such variable recruitment in turn may impact the size structure of local populations (Warner and Hughes 1989). The effect on size structure can have strong effects on rates of cannibalism (DeAngelis et al. 1979, Ricker 1954) providing a potentially

important interaction between habitat variation and the effect of cannibalism as they contribute to the dynamics of local populations.

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Table 1. Comparison of relative light intensity among habitat types in the field and experimental tanks. Values are the mean percent of surface light measured in each habitat.

HABITAT	DEPTH (M)	FIELD	TANK
Open Water	2	32.7	40.7
Understory	8	19.2	12.5
Upper Kelp	2	8.4	5.4
Lower Kelp	9	0.4	1.2

Table 2. Predator abundance at the no-cage and cage-control (half-cage) treatments. (A) Mean predator abundance is presented for the pilot study (1988) and the two recruitment trials (1989). Standard error of the mean is in parentheses. Means connected by underlines are not significantly different (repeated measures ANOVA). (B) Results of the repeated measures ANOVA. Parentheses refer to trial. Values were $\log(X + 0.3)$ transformed for analysis.

A.

YEAR	TRIAL	PREDATOR ABUNDANCE	
		NO-CAGE	HALF-CAGE
1988	1	3.47 (0.46)	4.75 (0.74)
1989	2	1.00 (0.18)	1.10 (0.39)
1989	3	1.10 (0.19)	2.47 (0.36)

B. ANOVA results:

SOURCE	TRIAL	DF	MS	F	P
CAGE	(1)	1	0.163	3.57	0.132
	(2)	1	0.021	0.10	0.759
	(3)	1	0.877	12.52	0.008
ERROR	(1)	4	0.046		
	(2)	8	0.210		
	(3)	8	0.070		
DAY	(1)	3	0.030	1.45	0.286
	(2)	2	0.282	1.76	0.203
	(3)	2	0.001	0.03	0.970
CAGE*DAY	(1)	3	0.023	1.13	0.382
	(2)	2	0.004	0.03	0.974
	(3)	2	0.060	1.36	0.284
RESIDUAL	(1)	10	0.021		
	(2)	16	0.160		
	(3)	16	0.044		

Table 3. Two-factor ANOVA for the effects of young-of-year size and habitat on the percent mortality of kelp bass in experimental tanks. Proportions were arcsin(square root) transformed for analysis.

SOURCE	DF	MEAN SQUARE	F	P
SIZE (S)	2	2.03	150.98	0.0001
HABITAT (H)	3	0.68	50.23	0.0001
S * H	5	0.36	26.72	0.0001

Table 4. Predation of young-of-year kelp bass among habitats by giant kelpfish. Values are the mean (1 S.E.) number of fish eaten (by all predators) during a 24 hr exposure to predators. 1 S.E. = one standard error of the mean. Underlined means are not significantly different from one another. The mean percent of individuals eaten per trial is also presented.

	<u>HABITAT</u>			
	No Algae	Upper Kelp	Lower Kelp	
MEAN	12.57	<u>2.5</u>	<u>3.0</u>	<u>1.67</u>
(1 S.E.)	(2.17)	(0.67)	(0.97)	(0.21)
PERCENT	31.4	6.3	7.5	4.2

Table 5. Distribution of predators of young-of-year kelp bass between habitats. Values are the mean density (fish X 60 m⁻³) of each predator species. Sample size = 26, 26 and 30 transects for the upper kelp, lower kelp and no-kelp (i.e., *Sargassum*) habitats, respectively.

SPECIES	HABITAT			HABITATS COMBINED
	UPPER KELP	LOWER KELP	NO KELP	
Giant kelpfish	0.92	0.62	0.67	0.73
Grass rockfish	0	0.08	0.03	0.04
Island kelpfish	0	1.38	1.03	0.82
Kelp bass	4.74	10.81	6.69	7.32
Kelp rockfish	0	0.12	0	0.04
Scorpionfish	0	0.38	0.43	0.32
Spotted kelpfish	0	0.15	0.9	0.38
Treefish	0	0.65	0.03	0.22
Total	5.82	14.04	9.83	

Table 6. Density of older kelp bass across algal habitats during the 1988 and 1989 settlement periods. Underlined means within the same year are not significantly different from one another.

YEAR	KELP BASS DENSITY (FISH PER 60 m ³)				P
	LOWER KELP	NO-KELP	UPPER KELP		
1988					
	MEAN	10.81	<u>6.69</u>	4.74	0.0001
	1 S.E.	0.87	0.66	0.82	
1989					
	MEAN	7.37	4.91	1.85	0.0001
	1 S.E.	0.43	0.47	0.23	

Table 7. The effect of predator presence and algal habitat on feeding rates of young-of-year kelp bass. (A) Mean (and 1 S.E.) bites per 4 min. Total is the total number of fish observed in each habitat/predator combination over two replicate trials. (B) Results of the two-factor ANOVA.

A.

ALGA	PREDATOR OCCURRENCE					
	PRESENT			ABSENT		
	MEAN	S.E.	TOTAL	MEAN	S.E.	TOTAL
<i>Sargassum</i>	3.7	0.8	35	3.5	0.5	25
<i>Macrocystis</i>	3.2	0.4	17	3.9	0.2	25

B. ANOVA Results:

SOURCE	DF	MS	F	P
PREDATOR (A)	1	0.003	0.45	0.54
ALGA (B)	1	0.004	0.68	0.46
A*B	1	<0.0001	0.01	0.92

Table 8. Effect of the presence of predators on the habitat use of naturally recruited young-of-year kelp bass. Values are the mean proportion of fish recorded in each habitat type ($n = 8$ censuses for each predator level). Total fish is the number of fish collected from each predator level at the end of the trial.

PREDATOR	HABITAT				TOTAL FISH	
	ALGAE PRESENT		ALGAE ABSENT			
	<i>Macrocystis</i>	<i>Sargassum</i>	OPEN WATER	SAND		
Present	0.74	0.18	0.0	0.08	101	
Absent	0.48	0.14	0.11	0.17	48	

FIGURE LEGENDS

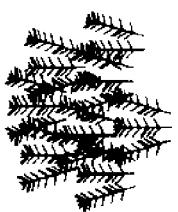
Figure 1. Predator exclusion manipulations on isolated reefs of *Sargassum palmeri*. (A) Total predator exclusion from reefs enclosed by 1 m³ cages of 5 X 5 mm sq nylon mesh netting, (B) cage-control allowing predator access and structural features (frame and netting) of exclusion cage, and (C) uncaged reefs allowing predator access to reef.

Figure 2. Density of kelp bass recruits on reefs of *Sargassum palmeri* on which predator access was manipulated. Plotted is the mean (\pm 1 S.E.) number of recruits per reef of each predator treatment. N = 5 replicate reefs per level. The experiments was repeated (trials) once; results are presented separately for each trial.

Figure 3. Vulnerability, measured as percent mortality, of young-of-year kelp bass to older (ca. 24-36 mo) kelp bass in three algal habitats and a no-algae control simulated in the laboratory. Plotted are the mean (\pm 1 S.E.) percent mortality of young-of-year kelp bass of three size classes over a 24 hr trial in each habitat type. Means denoted with similar letters are not significantly different. N = 6 replicate trials per mean.

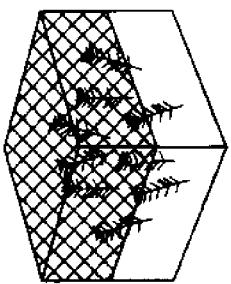
Figure 4. Effect of predator presence on the distribution of young-of-year kelp bass among algal and open (no structure) habitats. Plotted is the mean (\pm 1 S.E.) percent fish recorded in each habitat type. N = 6 replicate trials.

C.

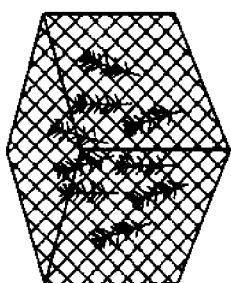


**NO CAGE
CONTROL**

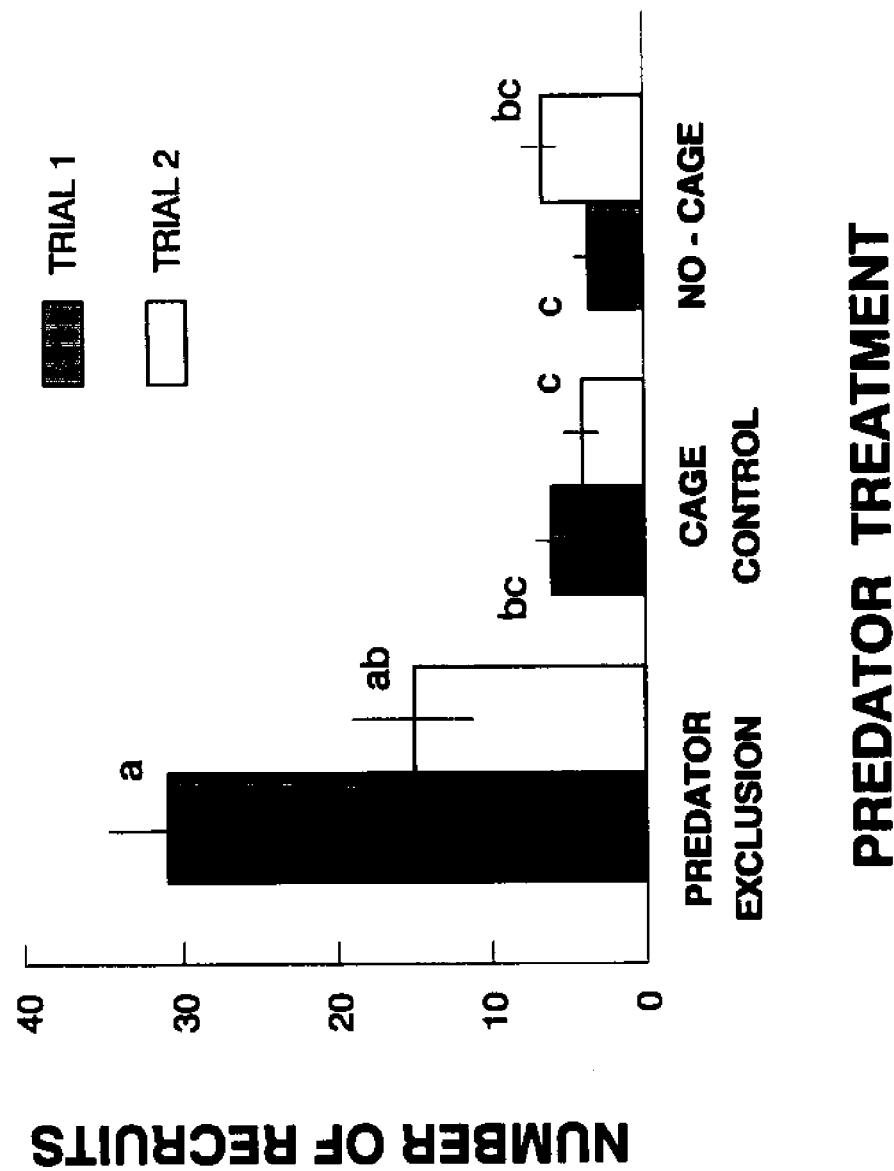
B.

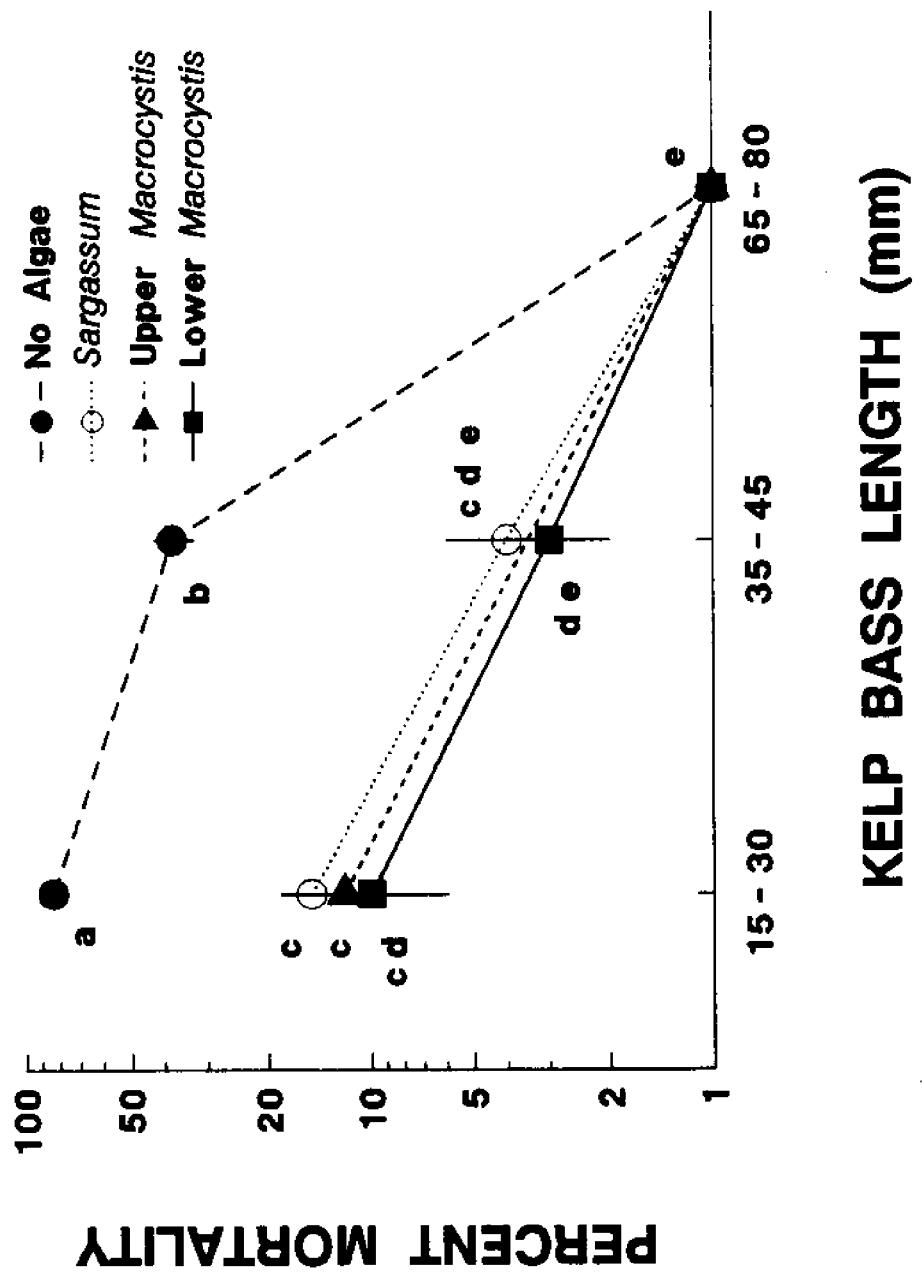


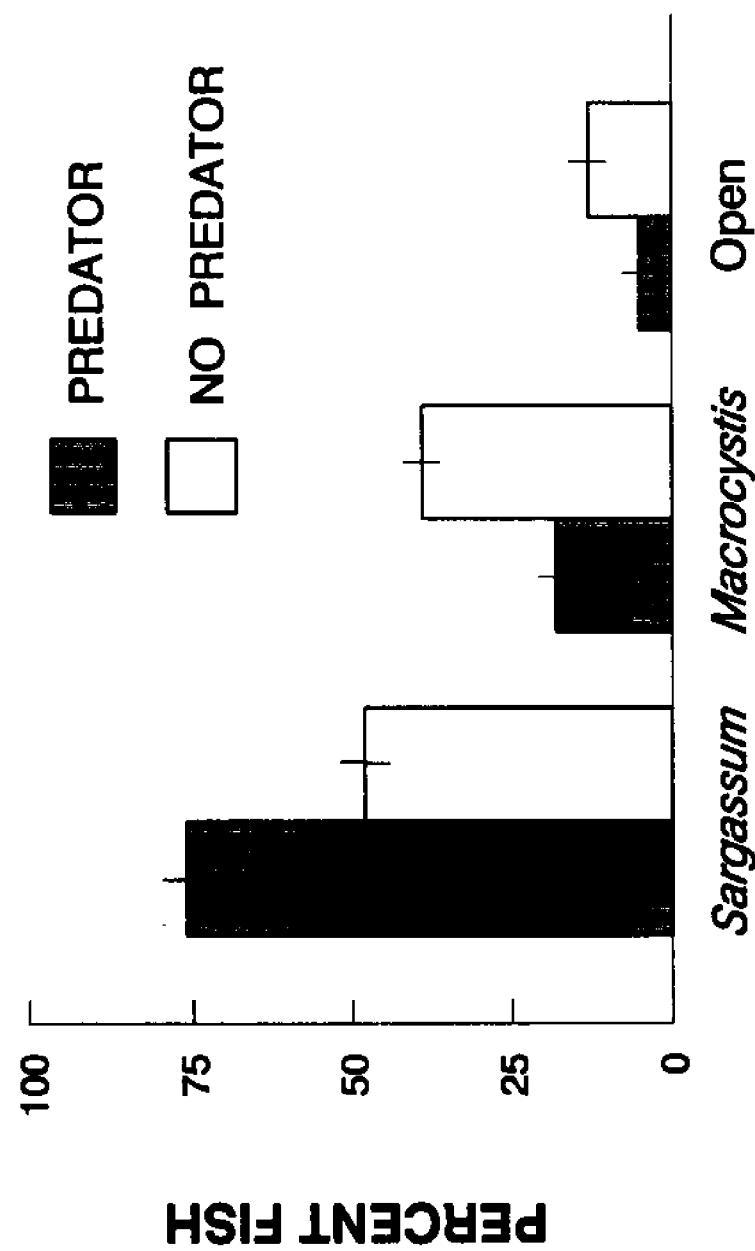
A.



**PREDATOR
EXCLUSION**







CHAPTER 4

THE RELATIONSHIPS BETWEEN SETTLEMENT HABITATS, FOOD SUPPLY AND GROWTH OF YOUNG KELP BASS

INTRODUCTION

Larval recruitment has been demonstrated to influence the structure, distribution and dynamics of marine reef fish populations (see reviews Doherty and Williams 1988, Richards and Lindeman 1987). Of the many factors thought to influence the distribution and magnitude of reef fish recruitment, supply of food in the benthic environment has received surprisingly little attention. Only four studies have addressed the effect of food abundance on the distribution and density of recruits (Jones 1984 a,b, 1986, Shulman 1984). Furthermore, consequences for the growth and survivorship of potential recruits of settlement among habitats that differ in food availability have not been examined. Food abundance in the benthic environment may influence recruitment by providing a behavioral cue for settlement. Limited abundance of food might also influence post-settlement survivorship directly via starvation or indirectly via reduced growth and increased vulnerability to predation. Several lines of evidence suggest that food abundance could influence the distribution and number of reef fish recruits. Increased growth of juvenile reef fish for which food abundance was experimentally supplemented (Jones 1986, Forrester 1990) and demonstrations of the density-dependent growth of recently settled reef fish (Jones 1987, 1990, Forrester 1990), both suggest that food may be limiting. Also, studies of patch choice by juvenile fish indicate that foraging success strongly influences habitat use (Mittlebach 1981, Schmitt and Holbrook 1985, 1988). Consequently, variation in food abundance may ultimately lead to differences in densities of recruits among habitats.

In this study I examine the relationship between foraging and food

abundance in different settlement habitats and their relations to growth performance of a temperate reef fish, the kelp bass (*Paralabrax clathratus*). Along the coast of southern California, planktonically-dispersed kelp bass larvae settle and recruit to shallow (< 20 m) algae-covered rocky reefs (Carr 1989, 1991). Densities of recently settled (< 1 wk) kelp bass vary among habitats on reefs. For instance, densities are highest in the upper portion of *Macrocystis* plants. Far fewer recently settled individuals occur in the lower portion of *Macrocystis* plants and in other types of foliose algae (Carr 1991). Here I determine whether these patterns of distribution are related to differences in food abundance and growth performance among these algal habitats.

METHODS

Study Area

All observations and experiments were conducted along the northwest coast of Santa Catalina Island (33°27'N : 118°29'W) which lies 40 km offshore of southern California. Along this portion of the coast, shallow (≤ 15 m) rocky reefs vary markedly from one another in the density of giant kelp, *Macrocystis pyrifera* (hereafter *Macrocystis*). *Macrocystis* plants grow vertically through the water column to form a surface canopy. Generally, beneath this canopy the cover of understory algae is sparse (Reed and Foster 1984, Schiel and Foster 1986, Carr 1989). In the absence of *Macrocystis*, reefs at Santa Catalina support dense stands of shorter (< 1 m tall) algae comprised of several species of which

the most abundant is *Sargassum palmeri*. Here, I define three major algal habitats- the upper portion of *Macrocystis* plants, including the canopy; the lower portion of *Macrocystis* plants, excluding the holdfast; and *Sargassum*-dominated stands which grow in the absence of *Macrocystis* (hereafter referred to as the upper *Macrocystis*, lower *Macrocystis* and *Sargassum* habitats, respectively).

Kelp bass settle from the plankton to shallow reefs at Santa Catalina Island during mid-July to September at a size of approximately 10 mm SL (standard length = anterior most portion of head to base of caudal fin). Regarding the three habitats defined above, the density of recently settled kelp bass (individuals ranging from 10 to 25 mm SL) is greatest in the upper half of *Macrocystis* plants (Carr 1991). By September, older, larger kelp bass recruits (individuals ranging from 50 to 60 mm SL) occur throughout the upper and lower half of *Macrocystis* plants and in adjacent *Sargassum* habitats. I distinguish between "recently settled" and "recruited" kelp bass for each of the observations and experiments described below.

I. Diel foraging activity and substrate use by kelp bass.

To determine the diel pattern of feeding activity of kelp bass recruits in among algal habitats, I sampled the feeding rate and stomach fullness of individuals in the upper *Macrocystis*, lower *Macrocystis* and *Sargassum* habitats. Feeding rate (bites per min) was recorded during 3 to 4 min observation periods of focal individuals within each of three time periods (morning = 0700-0900, mid-day = 1100-1300, afternoon = 1500-1800) and algal habitats (upper

Macrocystis, lower *Macrocystis* and *Sargassum*). The size of individuals sampled ranged from 30 to 50 mm SL. Fish smaller than this size were too closely associated with algal structure to observe without affecting their behavior. To control for temporal variation in plankton availability, I sampled equal numbers of individuals among the three algal habitats within each time period on each sampling date. Feeding rate was compared among diel periods and algal habitats with a two factor ANOVA. I used the REGWF a posteriori means comparison (SAS) for this and all following ANOVAs.

For each individual, numbers of bites taken from the water column and from algal substrates were recorded separately. Algal substrates used during foraging were *Sargassum palmeri* in the *Sargassum* habitat and *Macrocystis* in the upper and lower *Macrocystis* habitats. In order to avoid bias toward feeding in the water column, I attempted to sample fish closely associated with algal structure. Percent bites were arcsine-square root transformed and compared among diel periods and algal habitats with a two factor ANOVA.

I sampled stomach fullness (total prey weight per fish weight) at three time periods (dusk = within 1 hr before sunrise, mid-day, and evening = within 1 hr after sunset). The size range of individuals sampled was 10 to 40 mm SL. Individuals were sampled from each of the three algal habitats; however, because of difficulties in finding and collecting individuals in the *Sargassum* habitat early in the morning and in the evening, data for that habitat are for mid-day periods only. In each collection, fish were captured with hand held nets and placed in a vexar (5 mm mesh) tube. At the end of each sampling period, fish were brought to the surface and stomachs were immediately injected with 10% buffered formalin. I compared stomach fullness among time periods and

algal habitats for the upper and lower *Macrocystis* habitats with a two factor ANOVA and I compared stomach fullness among all three algal habitats at mid-day with a single factor ANOVA.

II. Relationship between algal habitat and dietary composition of recently settled and recruited kelp bass.

To determine if recently settled kelp bass on the upper and lower portions of *Macrocystis* plants exhibited differences in the taxonomic composition of their diets, I compared the percent weight and number of individuals of each prey taxon in kelp bass stomachs. Recently-settled kelp bass (10 to 22 mm SL) were collected with hand nets over a one week period during two diel periods (noon and dusk). Individuals were anesthetized with MS-222 and their stomachs injected with 10% buffered formalin. Stomachs were dissected using a dissecting scope. The biomass of prey items was estimated from prey length using length-weight relationships determined by Coyer (1979).

Because fish compared between algal habitats varied in body size and time of collection, I tested for the effects of all these variables on the composition of their diets. For dietary composition, the relative weight (total weight per prey taxon divided by total weight of all taxa combined) and number of individuals (total number per prey taxon divided by total number of all taxa combined) of each prey item were tested separately. The effects of algal habitat (upper vs lower *Macrocystis*), time of day (noon vs dusk), and kelp bass size (mm SL) on dietary composition were tested with a two factor (habitat and time of day) multivariate analysis of covariance (MANCOVA) using kelp bass size as

the covariate. I first tested for the three way and all two way interactions. Because none of the interactions were significant ($P > 0.12$ in all cases), I tested for habitat, time and size effects excluding interaction terms. If significant effects of a factor were detected, univariate tests were made to indicate which prey taxa differed between factor levels. Sample sizes were 28 and 21 individuals from the upper and lower *Macrocystis* habitats, respectively. Only taxa contributing ≥ 5 percent of the diet by weight or number for either habitat were included in the analysis.

To determine if kelp bass recruits on reefs with different algal habitats (*Macrocystis* vs *Sargassum*) differed in their diets, I collected recruits (50 to 60 mm SL) over a two-day period from three *Macrocystis* reefs and three *Sargassum* reefs ($n = 10$ individuals per reef). As before, relative weight and number of each prey taxon were used to compare the taxonomic composition of fish diets between algal habitats.

The effect of algal habitat (*Macrocystis* vs *Sargassum*) and kelp bass size (mm SL) on taxonomic composition of kelp bass diets were tested with a single factor (algal habitat) MANCOVA using kelp bass size as the covariate. Because the habitat by size interaction was not significant ($P = 0.64$ and $P = 0.65$ for the relative prey-taxon weight and number, respectively), I tested the habitat and size effects with a single factor MANCOVA excluding the interaction term. Univariate tests were made to indicate which prey taxa (among those contributing ≥ 5 percent of the diet by weight or number) differed between algal habitats.

III. Prey abundance in different algal habitats.

Differences in the taxonomic composition of kelp bass diets between algal habitats may simply reflect differences in the abundance of prey taxa. To determine if the diets of recently settled (in the upper and lower portions of *Macrocystis*) or recruited individuals (in *Macrocystis* or *Sargassum* habitats) reflected such differences in prey abundance, I sampled prey from algal substrates and the adjacent water column of each algal habitat.

Because four taxa that differed in the diets of recently settled kelp bass are entirely or partially planktonic, I estimated the density of these taxa in the water column adjacent to each algal habitat (i.e., upper and lower *Macrocystis* and *Sargassum*). Paired plankton samples were collected by pushing a 0.5 m dia 0.333 mm mesh plankton net for 60 m through each of the upper and lower halves of a *Macrocystis* forest and 1 to 2 m above a nearby *Sargassum* habitat. To minimize effects of the *Macrocystis* forest on plankton abundance, samples of planktonic prey above the *Sargassum* habitat were collected along side of, or upcurrent of, the nearest stand of *Macrocystis* plants. Plankton samples ($n=6$) were collected during mid-day on six different days from August to October and fixed in 10% buffered formalin within 15 min after collection.

Plankton samples were split with a Folsom plankton splitter in the laboratory and subsamples were sorted and counted using a dissecting scope. Density of each taxon was estimated by extrapolating counts by the number of plankton splits to the volume of water sampled (11.8 m^3) and standardized to number per m^3 . Because samples of each algal habitat always were taken within 0.5 hr of one another and replicates on different days, mean density

(individuals per m³) and weight (mg per m³) of each planktonic prey taxon could be tested for differences between the upper and lower *Macrocystis* habitats using a paired two sample t-test (n = 7). Differences in density and weight of each taxon were tested between *Macrocystis* and *Sargassum* habitats with a paired two sample t-test using the average of the paired samples from the upper and lower halves of the *Macrocystis* forest (n = 7). Because differences in size were determined for mysids but not for individual calanoids, harpacticoids or larvaceans, I tested differences in biomass between habitats for mysids only.

To estimate the density of prey (number and biomass) on the upper and lower halves of *Macrocystis* plants, I measured prey numbers and weight per kg *Macrocystis* and the mean biomass of *Macrocystis* (kg per m³) in each half of the water column. Thus, prey density per biomass of *Macrocystis* was estimated for upper and lower halves of plants by enclosing portions of *Macrocystis* plants (and associated prey) in 0.75 X 1.0 m Nitex bags of 0.5 mm mesh (n = 20 and 19, respectively). The length, number and wet weight of *Macrocystis* stipes (and blades) were recorded for each sample. Thus, the mean weights of a 1 m length of stipe (and blades), 0.247 ± 0.037 and 0.17 ± 0.017 SE kg, in the upper and lower halves of *Macrocystis* plants, respectively, were multiplied by the mean density of stipes to estimate the biomass of *Macrocystis* per m³ in each half of the water column. The density of stipes (number per m²) was measured at Habitat Reef where feeding observations were made and recently settled kelp bass were collected for stomach analyses. Density of stipes ≥ 1 m tall was measured 1 m above the bottom along six 30 m² transects. Because *Macrocystis* plants have fewer stipes at mid-depth than at the bottom, the density of stipes at mid-depth was then estimated from bottom densities using a mid-depth to

bottom stipe ratio determined from 46 randomly selected plants (ratio mean \pm 1 SE = 0.656 ± 0.024). Mean density (individuals per m³) and weight (mg per m³) of each algal-associated prey taxon were tested for differences between the upper and lower *Macrocystis* habitats using a two sample t-test ($n = 20$ and 19).

To estimate the density of prey (number and weight per m³) per algal type in the *Sargassum* habitat, I measured the biomass (kg per m³) of each alga and prey abundance (number of individuals and weight per kg) on the three predominant algae. Biomass per alga was determined from 78 0.5 m² quadrat samples, each at random distances along a 30 m transect ($n = 13$ transects), by removing all foliose algae from a quadrat, sorting to species and weighing damp. Because three species (*Sargassum palmeri*, *Zonaria palmata*, and *Dictyopterus* spp.) comprised 92% of the algal biomass in this habitat (see Results), I estimated the abundance of each prey taxon on these three species, and partitioned the remaining 8 % of the total algal biomass among them in proportion to their relative abundance. Prey abundance among the three algae was sampled (*Sargassum* $n = 15$, *Dictyopterus* $n = 15$, *Zonaria* $n = 12$) and processed as before. For each prey taxon, the mean densities (number and weight per 1 m³) were summed across the three algal species to estimate the total density for the habitat. Both absolute and relative densities (individuals per m³) and weights (mg per m³) of each algal-associated prey taxon were tested for differences between *Macrocystis* and *Sargassum* habitats using a t-test of a mean versus a single observation between the combined samples from the upper and lower *Macrocystis* habitats ($n = 39$) and the single summed estimate for the *Sargassum* habitat.

IV. Habitat effects on kelp bass growth.

A. Effect of algal habitat on growth of recently settled kelp bass.

To determine if the growth rate of recently settled (10-20 mm SL) kelp bass differed between the upper *Macrocystis*, lower *Macrocystis* and *Sargassum* habitats, I measured the growth of individuals caged in each algal habitat. Individuals were measured and placed into 0.3 m dia X 0.35 m ht (0.023 m³) cylindrical enclosures of 4 mm mesh netting, with drawstrings at each end to enclose fronds of *Macrocystis* in the upper and lower *Macrocystis* habitats. Clumps of *Sargassum* were simply placed inside enclosures in the *Sargassum* habitat. After 14 days, fish were collected from the enclosures and remeasured (to the nearest 0.5 mm SL) for growth. Two trials (1986 and 1987) were conducted and analyzed separately.

In the first trial (1986) individuals per cage initially ranged in size and density from 10 to 20 mm SL and 3 to 6, respectively. Although initial size distributions and densities were matched among the algal habitats, mortality during the experiment resulted in the exclusion of some cages from analysis (final n = 8 replicate cages per algal habitat). Consequently, mean (\pm 1 SE) individual size (mm SL) per cage differed among upper and lower *Macrocystis* and *Sargassum* habitats: 13.1 (\pm 0.83), 16.3 (\pm 1.16) and 15.8 (\pm 1.06), respectively. Although density of individuals differed among cages, it differed little among algal habitats: upper and lower *Macrocystis* and *Sargassum* habitats were 4.3 (\pm 0.45), 4.0 (\pm 0.38) and 4.4 (\pm 0.32) individuals per cage, respectively. Because both density and individual size differed among cages, I

tested for effects of these two variables on growth rate before testing for an effect of algal habitat. Then, because density but not size was strongly related to growth rate (see Results), I tested for a habitat effect with density as the covariate using single factor ANCOVA, with individuals nested within cages.

In the second trial (1987), the size and density of individuals ranged from 10 to 19 mm SL and 4 to 5 per cage, respectively. Even though no significant difference in growth rate was detected between individuals at these two densities in the previous trial, I tested for a habitat effect using ANCOVA with density as the covariate as in the previous trial. Of four replicate cages per algal habitat, one cage from the lower *Macrocystis* habitat was excluded from analysis because most of its fish died.

B. Growth of kelp bass recruits on *Macrocystis* and *Sargassum* covered reefs.

To determine the consequences of having recruited to reefs with or without *Macrocystis* on growth of young-of-year kelp bass, I compared growth rates among six reefs; three with and three without *Macrocystis* ($n = 10$ individuals per reef). All individuals, which ranged in mean size per reef from 48.5 to 51.5 mm SL, were collected within a two day period. Fish were aged using otolith (earbone) increments which are produced daily in kelp bass (Carr, unpublished data). The mean number of increments was calculated for each individual from six counts; three from each otolith (left and right sagitta). Counts included all increments from the perimeter to the center of the bone, including presettlement increments. Daily growth rate was calculated as the

length of the fish (mm SL) divided by the mean number of increments in its otolith. I tested for a difference in growth rate of fish among all six reefs with a single factor ANOVA and between reefs with and without *Macrocystis* ($n=3$) with a two sample t-test.

RESULTS

I. Diel foraging activity and substrate use by kelp bass.

The feeding rate (bites per min) of kelp bass recruits (length = 30 to 50 mm SL) differed among algal habitats and time of day. There were two different patterns. Kelp bass in two algal habitats, lower *Macrocystis* and *Sargassum*, exhibited very similar patterns of high feeding rates in the morning, gradually declining through the diurnal period (Figure 1). These two habitats contributed to a significant effect of time of day on feeding rate ($df = 2, F = 46.0, P = 0.0001$; REGWF means comparison: morning > mid-day > afternoon). In contrast, feeding rate in the upper *Macrocystis* habitat was markedly lower in the morning and declined little through the diurnal period (Figure 1). This difference contributed to a significant effect of algal habitat on feeding rate ($df = 2, F = 27.5, P = 0.0001$; REGWF means comparison: lower *Macrocystis* = *Sargassum* > upper *Macrocystis*) and a time of day by habitat interaction ($df = 4, F = 5.5, P = 0.0003$).

Differences in feeding rates among algal habitats corresponded to differences among habitats in use of the water column by foraging kelp bass

(Table 1). Individuals in the upper *Macrocystis* fed proportionately more from the algal substrates than individuals within the lower *Macrocystis* and *Sargassum* habitat ($df = 2$, $F = 20.5$, $P = 0.0001$; REGWF means comparison: upper *Macrocystis* > lower *Macrocystis* = *Sargassum*). Fish also fed proportionately less from algal substrates in the morning than later in the day (Table 1; $df = 2$, $F = 9.32$, $P = 0.0001$; REGWF means comparison: mid-day = afternoon > morning), and this pattern was consistent across all three algal habitats (i.e., no significant time of day by habitat interaction: $P = 0.62$).

The gradual decline in feeding activity through the day corresponded with a gradual increase in stomach fullness over the diurnal period (Figure 2). Stomach fullness of kelp bass in both *Macrocystis* habitats increased similarly (i.e., no significant habitat effect: $P = 0.436$, or time by habitat interaction: $P = 0.327$) from dawn to mid-day to dusk (time effect: $df = 2$, $F = 31.59$, $P = 0.0001$, REGWF means comparison: dusk > mid-day > dawn). This gradual increase in stomach fullness over the day indicates that recently settled kelp bass do not feed at night, then begin feeding at sunrise, and feed continuously through the diurnal period. At mid-day, the stomach fullness of fish in the *Sargassum* habitat was intermediate between that of individuals in the upper and lower *Macrocystis* habitats (Figure 2). Therefore, although individuals fed at different rates among some algal habitats, differences in feeding rate appear to be compensated by differences in substrate use, in that individuals from the upper and lower *Macrocystis* habitats have converged in stomach fullness by the end of the day.

II. Relationship between algal habitat and dietary composition of recently settled and recruited kelp bass.

The taxonomic composition of the diet of recently settled kelp bass differed between upper and lower *Macrocystis* habitats. Diets in the upper habitat included relatively more (by weight and number of individuals) calanoid copepods and larvaceans (Figure 3, Tables 2 and 3). In contrast, kelp bass in the lower portions of *Macrocystis* ate relatively more (by weight and number of individuals) harpacticoid copepods.

The relative weight and number of individuals of prey taxa in the diet of recently settled kelp bass also varied with predator size (mm SL). Smaller kelp bass consumed relatively more (number of individuals) harpacticoids than did larger kelp bass, explaining the greater relative biomass of harpacticoids in smaller kelp bass (Figure 4). Only larger kelp bass ate shrimp, where large individual size explained the strong relationship between fish size and relative biomass of shrimp in the diet (Figure 4).

There were also marked differences in diets of kelp bass that recruited to reefs of *Macrocystis* or *Sargassum*. In *Macrocystis* habitats, recruits consumed relatively more (by weight and number of individuals) gammarids and mysids, whereas recruits in *Sargassum* habitats ate relatively more caprellids (Figure 5, Tables 4 and 5). Recruits in *Macrocystis* also consumed relatively more larvaceans (number of individuals) but because larvaceans are so small, this difference in number of individuals was not reflected in a significant difference in larvacean biomass.

III. Prey abundance in different algal habitats.

A. Upper vs lower *Macrocystis*.

Of the three planktonic taxa whose relative abundance in fish diets differed between the upper and lower portions of *Macrocystis*, only harpacticoid copepods differed in abundance. Harpacticoid copepods were both more abundant in the environment (number per 1 m³) and in fish diets in the lower than in the upper half of the water column (Table 6). Although mean densities of calanoid copepods and larvaceans tended to be greater in the upper water column, reflecting their greater abundance in kelp bass diets, the difference was not significant (Table 6), perhaps because the low sample size ($n = 7$) and high within-sample variance (i.e., low statistical power).

Neither the relative nor absolute density or biomass of algal-associated prey differed between the upper and lower halves of the *Macrocystis* forest. Relative abundances were so similar as to obviate statistical comparison (Figure 6). The density of only one prey, caprellid amphipods, differed significantly between upper and lower halves of the forest (Figure 7). Although caprellids were more abundant in the lower half, this was not reflected in fish diets because so few of this prey were consumed (i.e., less than 5% of the diet).

B. *Macrocystis* vs *Sargassum* habitats.

Reflecting the observed dietary differences, the density and biomass of mysids collected in plankton samples were marginally greater ($P = 0.093$ and

0.075, respectively) in *Macrocystis* forests than in *Sargassum* habitats (Table 7). Although no such dietary correspondence was detected for larvaceans, the fact that habitat differences in larvaceans were not detected may have been due to the low sample size and high within-sample variability (Table 7).

Three algal species, *Sargassum palmeri*, *Zonaria palmata*, and *Dictyopterus* spp., comprised 92% of the algal biomass of the *Sargassum* habitat (55, 29 and 9 percent, respectively). Mean (\pm 1 SE) biomass of all foliose algae combined was 4.69 ± 0.50 kg/ m³.

The density (individuals per m³) and weight (mg per m³) of every prey taxon except mysids was greater in the *Sargassum* than the *Macrocystis* habitat (Figure 8; P < 0.002 in all cases), with mysids significantly greater in *Macrocystis* (Figure 8; P < 0.001). This, also with relative abundance differences, was reflected by kelp bass diets (Figure 9; T = 6.24, P < 0.001 and T = 8.29, P < 0.001, for density and biomass, respectively). The greater relative and absolute abundance of caprellids in the *Sargassum* habitat were also reflected in kelp bass diets (Figure 9; T = 3.90, P < 0.001 and T = 131.8, P < 0.001, for density and biomass, respectively). On the other hand, although gammarids were relatively greater in diets of fish in the *Macrocystis* habitat, their absolute abundance was higher in the *Sargassum* habitat (Figure 9; T = 1.38, P = 0.176, and T = 1.78, P = 0.08, for density and biomass, respectively).

IV. Habitat and density effects on kelp bass growth.

A. Effect of density, algal habitat, and size on growth of recently settled kelp bass.

In the first trial (1986), fish density strongly affected growth rate (Figure 10), although fish size did not ($r^2 = 0.10$, $df = 23$, $P = 0.07$), possibly because fewer larger fish were placed together in cages than were smaller fish (i.e., size and density covaried: $r^2 = 0.18$, $df = 23$, $P = 0.023$). Thus, there was no density by size interaction in the two-factor analysis ($P = 0.37$) and only the density effect remained strongly significant ($P = 0.001$). Therefore, in a test for an effect of algal habitat using only density as a covariate, habitat showed no significant effect on growth rate ($df = 2$, $F = 1.11$, $P = 0.35$) with no significant habitat by density interaction ($df = 2$, $F = 1.04$, $P = 0.37$).

In the second trial in 1987, however, an effect of algal habitat was detected over a more restricted range of density (4 and 5 individuals per cage) as the covariate ($df = 2$, $F = 6.45$, $P = 0.026$). No density effect ($df = 1$, $F = 1.99$, $P = 0.20$) or density by habitat interaction was detected ($df = 2$, $F = 1.36$, $P = 0.34$). Growth was similar between the upper *Macrocystis* and *Sargassum* habitats and significantly greater in these two habitats than in the lower *Macrocystis* habitat (Figure 11; Tukey a posteriori means comparison).

B. Growth of kelp bass recruits on *Macrocystis* and *Sargassum* covered reefs.

Although growth rate of kelp bass recruits differed among reefs (Figure 12; $df = 5$, $F = 8.66$, $P = 0.0001$), these differences were apparently not related to the presence or absence of *Macrocystis* ($df = 4$, $t = 0.606$, $P = 0.58$). Thus, there seems to be little effect of *Macrocystis* itself on the pattern of growth rates of recruits among reefs (Figure 12).

DISCUSSION

In three of the total four published studies of the effect of food abundance on reef fish recruitment, no evidence for increased recruitment with increased food abundance was found (Jones 1984b, 1986, Shulman 1984). Jones' (1984a,b) studies of the patterns of larval recruitment of a temperate labrid, *Pseudolabrus celidotus*, off New Zealand is of a system very similar to that of the kelp bass. Like kelp bass, *P. celidotus* recruits to a kelp, *Ecklonia radiata*, and feeds on algal-associated calanoid copepods and gammarid amphipods. In an earlier study, Jones (1984b) found a positive relationship between food abundance and recruit density between a shallow (food rich) and deep (food poor) site. However, on closer examination, prey abundance (gammarid amphipods) was actually greater on small red algae in adjacent boulder and rock flat habitats than on the *Ecklonia* to which fish recruited. Unfortunately, calanoid abundance was not measured among all three habitats.

Nonetheless, the depth distribution of recruits may be due to factors other than food availability.

Shulman (1984) manipulated abundances of algae and a variety of encrusting and coral-associated mobile invertebrates on patches of *Strombus gigas* shells and the coral *Porites porites*. The negative results of Shulman's manipulations were convincing, having been sustained over three different experiments involving two substrates, and recruits of both herbivorous and omnivorous reef fishes.

Jones (1986) compared the growth rate of juveniles of a planktivorous reef fish, *Pomacentrus amboinensis*, on deep coral reefs, to which it preferentially recruits, with that on shallow reefs. Growth rates and survival of juveniles on deep reefs were higher than on shallow reefs. Food was demonstrated to be limiting by an increased growth rate relative to controls, on both shallow and deep reefs when food was supplemented. Food abundance was never measured between shallow and deep reefs. Recruits on shallow reefs should exhibit a disproportionately higher growth rate than those on deep reefs given the same supplement, yet recruits on shallow reefs did not show disproportionately greater growth as expected. Therefore the higher growth rate on deeper reefs where recruitment was greater may reflect differences other than food availability.

Four lines of evidence in the present study indicate that the greater recruitment of kelp bass to *Macrocystis* relative to *Sargassum* is not strongly influenced by differences in food abundance or growth performance. First, the density of all algal-associated prey taxa except mysids was greater in *Sargassum* than *Macrocystis*. Although this increase in mysid abundance was reflected in a

greater relative abundance of mysids in the diet of kelp bass in *Macrocystis*, mysids constituted only 10% of the diet. Mysids were also the only taxon in the plankton whose density was greater in the *Macrocystis* habitat. Overall, the combined abundance of algal-associated and planktonic prey was much greater in the *Sargassum* than in the *Macrocystis* habitat.

Second, by mid-day, stomach fullness of individuals from *Sargassum* and *Macrocystis* habitats were very similar. Kelp bass recruits are diurnal foragers and they are most active during the first half of the day. Third, growth rates of recently settled kelp bass (10 to 20 mm SL) did not differ between the upper *Macrocystis* and *Sargassum* habitats and were actually greater in *Sargassum* than in the lower *Macrocystis* habitat during one trial. Fourth, although older kelp bass recruits (50 to 60 mm SL) exhibited differences in growth among reefs, there was no evidence that growth was greater on reefs with *Macrocystis* than reefs with *Sargassum*. Therefore, in terms of food abundance and growth, the *Sargassum* habitat appears to be of comparable or greater quality than the *Macrocystis* habitat and the greater recruitment to *Macrocystis* habitats is not explained by differences in food abundance.

Comparisons of growth of kelp bass in *Sargassum* and *Macrocystis* habitats could potentially be confounded by differences in density of recruits. Because recruit density is generally higher on reefs with *Macrocystis*, higher food abundance in *Macrocystis* habitats may be countered by greater competition among recruits and reductions in growth. Indeed, I detected a strong density effect on growth of recently settled kelp bass in experimental cages. Nonetheless, when density was accounted or controlled for in the first and second trials of the growth experiments involving recently settled kelp bass,

growth was no greater in *Macrocystis* than *Sargassum*. Because growth rates (relative to body size) are greater for these smaller individuals, individuals of this smaller size range are probably more sensitive to factors influencing growth.

Within *Macrocystis* forests, the relationship between food abundance and growth is less clear. Although growth of recent settlers was higher in the upper *Macrocystis* (in one of two experimental trials), it is not clear that food abundance was greater there. On *Macrocystis* plants, the only prey taxon that differed in density between the upper and lower half of plants was caprellid amphipods. Although caprellids were more abundant in the lower habitat, this difference did not appear to affect the overall energy content of the diets of recently settled kelp bass because caprellids constituted so little (< 5%) of the diet. In the plankton, the only prey that differed in abundance between the upper and lower water column was harpacticoid copepods. Harpacticoids were also more abundant in the lower half of the *Macrocystis* forest and this difference was clearly manifested in their greater relative abundance in the fish's diet. These differences in food abundance suggest that growth could be greater in recently settled individuals in the lower *Macrocystis* habitat. It is possible that the lower growth rates of individuals caged there may be an artifact of restricted movement in cages; had these fish moved freely within that habitat, perhaps foraging success would have been comparable to that in the upper half of plants.

In contrast, planktonic calanoid copepods and larvaceans constituted a greater proportion of the diet of kelp bass recently settled in the upper portion of *Macrocystis* plants. Plankton samples did not reveal significantly greater densities of these two taxa in the upper half of the forest, although the short

duration of these samples probably did not reflect possible differences in current speeds and the rate of delivery of planktonic prey. All else equal, drag along the bottom results in slower current speeds (and plankton delivery) lower in the water column (Jackson and Winant 1983). This appears to be accentuated within the small (< 50 m wide) beds along Santa Catalina exposed to strong longshore tidal currents. Therefore the higher growth rate of recently settled bass caged in the upper half of the water column may reflect the higher rates of plankton delivery to this habitat.

That growth of both recently settled and older recruits was no greater in *Sargassum* habitats where prey abundance was greatest suggests two possible conclusions. Food abundance as measured there may not be an accurate indicator of its availability to kelp bass foraging in these different algal habitats. However, differences in the relative abundance of particular prey among algal habitats were often reflected in the relative abundance of these taxa in kelp bass diets, suggesting that food abundance does indeed reflect availability to foraging kelp bass. An alternative conclusion is that food is super abundant in both *Macrocystis* and *Sargassum* habitats and fish are everywhere satiated. This is supported by the similar stomach fullness of individuals from all three algal habitats. This, of course, is not to say that food is never limiting, only that it did appear to be during my study.

In conclusion, the greater recruitment of kelp bass to *Macrocystis* habitats but greater abundance of food in *Sargassum* habitats strongly suggest that differences in food abundance do not influence density or the early growth performance of individuals settled there. Thus, previous alternative explanations for the greater recruitment of kelp bass to the upper portions of

Macrocystis appear more likely: The greater height of *Macrocystis* creates greater plant-surface exposure to settling kelp bass from a greater portion of the water column than does the shorter algae of the *Sargassum* habitat (Carr 1991). Also, having recently settled in the upper half of *Macrocystis* plants, recruits are exposed to fewer predators than settlers in the lower *Macrocystis* and *Sargassum* habitats (Carr 1991). The conclusions from my study corroborate those of Shulman (1984) and Jones (1984b), suggesting that for the few species examined to date, factors other than food abundance play a greater role in determining differences in recruitment among habitats. Common among all three studies was evidence that algae provide a refuge for settling and/or recently settled individuals. Similarly, juveniles of the planktivorous blacksmith, *Chromis punctipinnis*, restrict their movement from shelter sites in the midst of a *Macrocystis* forest in spite of the greater plankton abundance along the outer edges (Bray 1981). Nonetheless it may be worthwhile to pick for future study, species for which shelter is not so critical for their survival. In the absence of shelter limitation, food abundance may be revealed to have detectable effects on the distribution of reef fish recruitment.

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Table 1. Percent bites from algal substrates by foraging young-of-year kelp bass in each of three algal habitats. Fish size ranged from 30 to 50 mm SL. Sample size ranged from 20 to 54 individuals for each habitat-diel period combination (total number of individuals = 303).

TIME OF DAY	<u>ALGAL HABITAT</u>		
	<u>Upper</u> <i>Macrocystis</i>	<u>Lower</u> <i>Macrocystis</i>	<i>Sargassum</i>
	MEAN (SE)	MEAN (SE)	MEAN (SE)
MORNING	26 (6.8)	5 (3.0)	1 (0.6)
MID-DAY	50 (7.2)	19 (5.5)	17 (4.3)
AFTERNOON	44 (9.1)	13 (6.1)	25 (8.5)

Table 2. Results of the multivariate analysis of covariance (MANCOVA) test of the effect of habitat (upper vs lower *Macrocystis*), time of collection (noon vs dusk) and kelp bass size (mm SL) on the taxonomic composition (proportion by weight) of prey in the diet of recently settled kelp bass (10 to 22 mm SL). Results of the separate univariate analyses of the effect of habitat and kelp bass size are presented by prey taxon below. Degrees of freedom for all univariate tests are 1 and 45. N = 21 and 28 kelp bass from the upper and lower *Macrocystis* habitats, respectively. Prey means are presented in Figure 3.

MULTIVARIATE RESULTS:

FACTOR	DF	PILLAI TRACE	F	P
Habitat	6, 40	0.295	2.79	0.023
Size	6, 40	0.438	5.19	<0.001
Time	6, 40	0.08	0.576	0.747

UNIVARIATE RESULTS:

PREY SPECIES	HABITAT	P VALUES	
			SIZE
Gammarid amphipods	0.682		0.722
Calanoid copepods	0.007		0.314
Shrimp	0.34		<0.001
Mysids	0.235		0.355
Larvaceans	0.019		0.641
Harpacticoid copepods	0.021		0.006

Table 3. Results of the multivariate analysis of covariance (MANCOVA) test of the effect of habitat (upper vs lower *Macrocystis*), time of collection (noon vs dusk) and kelp bass size (mm SL) on the taxonomic composition (proportion by number of individuals) of prey in the diet of recently settled kelp bass (10 to 22 mm SL). Results of the separate univariate analyses of the effect of habitat and kelp bass size are presented by prey taxon below. Degrees of freedom for all univariate tests are 1 and 45. N = 21 and 28 kelp bass from the upper and lower *Macrocystis* habitats, respectively. Prey means are presented in Figure 3.

MULTIVARIATE RESULTS:

FACTOR	DF	PILLAI TRACE	F	P
Habitat	6, 40	0.45	5.452	<0.001
Size	6, 40	0.339	3.414	0.008
Time	6, 40	0.117	0.886	0.514

UNIVARIATE RESULTS:

PREY SPECIES	HABITAT	P VALUES	SIZE
Gammarid amphipods	0.909		0.086
Calanoid copepods	0.014		0.481
Shrimp	0.872		0.004
Mysids	0.235		0.355
Larvaceans	0.045		0.687
Harpacticoid copepods	<0.001		0.014

Table 4. Results of the multivariate analysis of covariance (MANCOVA) test of the effect of algal habitat (*Macrocystis* vs *Sargassum*) and kelp bass size (mm SL) on the taxonomic composition (proportion by weight) of prey in the diet of kelp bass recruits (50 to 60 mm SL). Results of the univariate analyses of habitat effect are presented by prey taxon below. Degrees of freedom for all univariate tests are 1 and 57. N = 30 kelp bass per algal habitat. Prey means are presented in Figure 5.

MULTIVARIATE RESULTS:

FACTOR	DF	PILLAI TRACE	F	P
Habitat	6, 52	0.424	6.38	<0.001
Size	6, 52	0.189	2.02	0.079

UNIVARIATE RESULTS:

PREY SPECIES	F	P
Gammarid amphipods	11.45	0.001
Calanoid copepods	3.47	0.068
Shrimp	0.57	0.453
Caprellid amphipods	11.88	0.001
Mysids	7.02	0.01
Larvaceans	2.87	0.096

Table 5. Results of the multivariate analysis of covariance (MANCOVA) test of the effect of algal habitat (*Macrocystis* vs *Sargassum*) and kelp bass size (mm SL) on the taxonomic composition (proportion by number of individuals) of prey in the diet of kelp bass recruits (50 to 60 mm SL). Results of the univariate analyses of habitat effect are presented by prey taxon below. Degrees of freedom for all univariate tests are 1 and 57. N = 30 kelp bass per algal habitat. Prey means are presented in Figure 5.

MULTIVARIATE RESULTS:

SOURCE	DF	PILLAI TRACE	F	P
Habitat	6, 52	0.31	3.89	0.003
Size	6, 52	0.098	0.937	0.476

UNIVARIATE RESULTS:

PREY SPECIES	F	P
Gammarid amphipods	6.06	0.017
Calanoid copepods	2.55	0.116
Shrimp	2.16	0.147
Caprellid amphipods	7.22	0.009
Mysids	4.03	0.05
Larvaceans	8.2	0.006

Table 6. Density (individuals per m³) of planktonic prey of recently settled kelp bass in the upper and lower portions of *Macrocystis* forests. Presented is the mean (\pm 1 SE) density from seven plankton tows in each half of the water column and the results of a paired t-test of the differences of paired samples from each sampling date.

Taxon	<i>Macrocystis</i> Habitat		T	P
	Upper	Lower		
Calanoids	25.3 (6.1)	19.2 (5.7)	0.64	0.545
Harpacticoids	0.4 (0.2)	1.9 (0.6)	2.94	0.026
Larvaceans	2.0 (1.3)	1.2 (0.9)	1.55	0.173
Mysids	0.3 (0.2)	0.8 (0.3)	1.85	0.114

Table 7. Density (individuals per m³) of planktonic prey of kelp bass recruits in the *Sargassum* and *Macrocystis* algal habitats. Presented is the mean (\pm 1 SE) density from seven plankton tows in each algal habitat and the results of a paired t-test of the differences of paired samples from each sampling date.

Taxon	Algal Habitat		T	P
	<i>Macrocystis</i>	<i>Sargassum</i>		
Calanoids	22.2 (3.5)	24.4 (11.4)	0.20	0.852
Harpacticoids	1.2 (0.4)	0.3 (0.1)	2.07	0.084
Larvaceans	1.6 (1.1)	2.5 (1.4)	0.95	0.377
Mysids	0.54 (0.2)	0.05 (0.04)	2.15	0.075

FIGURE LEGENDS

Figure 1. Relationship between time of day and feeding rate of kelp bass recruits in each of three algal habitats. Plotted is the mean (± 1 SE) feeding rate of individuals (see text for sample sizes).

Figure 2. Relationship between stomach fullness and time of day for kelp bass in the upper and lower *Macrocystis* algal habitats. Stomach fullness of individuals within the *Sargassum* habitat is given for mid-day only. Plotted is the mean (± 1 SE) stomach fullness of 12 to 16 individuals per habitat-time sample.

Figure 3. Taxonomic composition of the diet of recently-settled kelp bass (10 to 22 mm SL) in the upper and lower portions of *Macrocystis* plants. Plotted are the mean (± 1 SE) percent weight and number of individuals for each habitat. GAM = gammarid amphipods, CAL = calanoid copepods, HRP = harpacticoid copepods, SHR = shrimp, LRV = larvaceans, and MYS = mysids. N = 28 and 21 kelp bass from the upper and lower *Macrocystis* habitats, respectively.

Figure 4. Relationship between kelp bass size and the relative abundance (percent weight and number) of harpacticoid copepods and shrimp in the diet of recently settled kelp bass. N = 28 and 21 kelp bass from the upper and lower *Macrocystis* habitats, respectively.

Figure 5. Taxonomic composition of the diet of kelp bass recruits (50 to 60 mm SL) on *Macrocystis* and *Sargassum* covered reefs. Plotted are the mean (± 1 SE) percent weight and number of individuals for each algal habitat.

GAM = gammarid amphipods, SHR = shrimp, CAL = calanoid copepods, CAP = caprellid amphipods, MYS = mysids, and LRV = larvaceans. N = 30 kelp bass from each algal habitat.

Figure 6. Mean (± 1 SE) relative density (individuals per m^3) and weight (mg per m^3) of the five most abundant algae-associated prey taxa on the upper and lower halves of *Macrocystis* plants. N = 20 and 19 samples from the upper and lower halves of *Macrocystis* plants, respectively. See Figure 5 for abbreviations of prey taxa.

Figure 7. Mean (± 1 SE) density and total weight of the five most abundant algal-associated prey taxa on the upper and lower halves of *Macrocystis* plants. n = 20 and 19 samples from the upper and lower halves of *Macrocystis* plants, respectively. See Figure 5 for abbreviations of prey taxa.

Figure 8. Density and total weight of the five most abundant algae-associated prey taxa in the *Macrocystis* and *Sargassum* habitats. Values for the *Macrocystis* habitat are the mean (± 1 SE) of 39 samples. Values for the *Sargassum* habitat are the sum of means across algal species. See Figure 5 for abbreviations of prey taxa.

Figure 9. Relative density and total weight of the five most abundant algal-associated prey taxa in the *Macrocystis* and *Sargassum* habitats. Values for the *Macrocystis* habitat are the mean (± 1 SE) of 39 samples. Values for the *Sargassum* habitat are the sum of means across algal species. See Figure 5 for abbreviations of prey taxa.

Figure 10. Effect of density on growth rate of recently settled kelp bass. Values plotted are the mean growth rate of individuals per cage. $n = 24$ cages, $r^2 = 0.497$, $df = 23$, $P < 0.001$.

Figure 11. Effect of algal habitat on growth rate of recently settled kelp bass. Plotted are the mean (± 1 SE) growth rate of individuals among replicate cages in each algal habitat. $N = 4$, 3, and 4 cages for the lower *Macrocystis*, *Sargassum*, and upper *Macrocystis* habitats, respectively. Means with the same letter are not significantly different from one another.

Figure 12. Comparison of growth rate of kelp bass recruits among reefs. Presented is the mean (± 1 SE) growth rate for 10 individuals per reef. Shaded and unshaded histograms indicate reefs with or without *Macrocystis*, respectively. Means not significantly different from one another are connected by horizontal lines at top of figure. Reefs I through VI are Big Fisherman Cove, Intakes, Habitat Reef, Ripper's, Lion's Head West, and Lion's Head East, respectively.

