

PREDATOR RESPONSES, PREY REFUGES, AND DENSITY-DEPENDENT MORTALITY OF A MARINE FISH

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Abstract. Detection of density dependence in animal populations is a primary goal of population ecology, and the processes causing density dependence play a major role in population regulation. Predation can strongly regulate populations by populational and behavioral responses of predators to their prey. Here I evaluate the existence and strength of density-dependent mortality in local populations of a reef fish, the kelp perch (*Brachyistius frenatus*), caused by its predator, the kelp bass (*Paralabrax clathratus*). Specifically, I examine both the functional response and a potential aggregative response by kelp bass as mechanisms underlying predator-induced density-dependent mortality.

I calculated the per capita mortality of kelp perch as a result of the functional response of its predator by subjecting a range of densities of kelp perch to a low, constant number of kelp bass and different amounts of giant kelp (*Macrocystis pyrifera*) as habitat structure and a potential prey refuge. The potential for an aggregative response by kelp bass was determined by exposing densities of kelp perch to natural levels of kelp bass in the field. Per capita mortality of kelp perch in the laboratory was inversely density dependent to density independent with increasing habitat structure. By contrast, per capita mortality in the field was strongly density dependent, with evidence for an aggregative response by kelp bass. Furthermore, emigration and other nonpredatory losses of kelp perch from field plots were negligible, indicating that the product of the functional and aggregative responses by kelp bass induced density-dependent mortality in kelp perch. My results indicated that increasing habitat structural complexity at low densities of kelp perch, coupled with a strong aggregative response by kelp bass, was responsible for the observed pattern of density-dependent mortality. In addition, the distribution and relative abundances of kelp perch and kelp bass at larger spatial scales (entire reefs) were consistent with predation as an important process structuring local populations of kelp perch. The contrasting patterns of short-term per capita mortality found here underscore the need to evaluate both the functional and aggregative responses of predators to their prey. Ultimately, the pattern of mortality expressed will be determined by the relative strengths of these behavioral responses and the degree to which habitat structure provides an effective prey refuge.

Key words: *aggregative response; Brachyistius frenatus; density-dependent mortality; functional response; habitat structure; kelp (Macrocystis pyrifera); Paralabrax clathratus; population regulation; predation; prey refuges; reef fish.*

INTRODUCTION

The processes by which populations vary in abundance in space and time constitute fundamental areas of ecological research, and identifying the mechanisms through which such processes operate is crucial to understanding population dynamics (Cappuccino and Price 1995). A major issue is whether these processes operate in a density-dependent manner, which in turn provides the basis for population regulation (Hassell 1978, 1986, Murdoch 1994, Turchin 1995). Density dependence can exist spatially as differences in demography between local populations and temporally as changes in demography within a population, and is manifest as increasing per capita mortality and emi-

gration rates or decreasing per capita fecundity and immigration rates as a population increases in size (Cappuccino and Price 1995, Begon et al. 1996, Sinclair and Pech 1996).

Density-dependent processes often have their origins in biotic interactions within and between species, especially competition and predation (Cappuccino and Price 1995, Begon et al. 1996). Predation has been examined for both its direct and indirect effects on populations (Taylor 1984, Sih et al. 1985, Kerfoot and Sih 1987, Hixon 1991, Wootton 1994). Importantly, the dynamics and stability of prey populations are influenced by long-term populational and short-term behavioral responses of predators (Hassell 1966, 1978, Hassell and May 1974, Murdoch and Oaten 1975, Murdoch and Bence 1987). Strictly defined, the numerical (Hassell 1966, 1978, Murdoch and Oaten 1975) and developmental (Murdoch 1971) responses of predators to higher prey densities increase the predator's birth

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and growth rates, respectively. By contrast, the functional and aggregative responses of predators are more immediate behavioral responses. The functional response predicts a predator's consumption rate as a function of prey density (Solomon 1949, Holling 1959), whereas an aggregative response results in a redistribution of predators to more profitable foraging areas with higher prey concentration (Hassell 1966, Hassell and May 1974).

These responses all have the potential to induce density-dependent mortality in prey populations. The effects of a functional response may be that per capita mortality of prey (i.e., individual predation risk) increases or remains unchanged, but will ultimately decline with an increase in prey density (i.e., the dilution effect). Only the accelerating region of the sigmoidal Type III functional response curve can cause density dependence and has the potential to stabilize a population (Murdoch and Oaten 1975, Taylor 1984). With an aggregative response, per capita mortality may be equivalent or increase across a range of prey density, thus causing density dependence. In this manner, the product of the functional and aggregative responses determines predation intensity (e.g., Turchin and Kariva 1989) and can result in compensatory mortality, caused by different combinations of the functional and aggregative responses (Hassell 1978).

Despite considerable theory (Murdoch and Oaten 1975, Taylor 1984) and the perception that predation induces density dependence and regulates prey populations, there remains scant empirical evidence to support this view in several ecosystems (Cappuccino and Price 1995). However, there has been considerable research concerning the effects of predation on freshwater and marine fish populations (Houde 1987, Bailey and Houde 1989, Hixon 1991, Heath 1992, Bailey 1994, Leggett and DeBlois 1994, Chambers and Trippel 1997) including size structure of predators and prey (Werner and Gilliam 1984, Crowder et al. 1994, Juanes 1994, Paradis et al. 1996, Rice et al. 1997, Sogard 1997), cohort development (Houde 1987, 1997, DeAngelis and Gross 1992, Bradford and Cabana 1997), indirect and interactive effects of predation and habitat structure (Werner et al. 1983, Mittelbach and Chesson 1987, Stein et al. 1988, Werner and Hall 1988, Heck and Crowder 1991, Mittelbach and Osenberg 1993, Persson and Eklov 1995, Persson and Crowder 1998), and nonadditive effects of different predators (Crowder et al. 1997, Hixon and Carr 1997). In contrast, there is only recent direct or suggestive evidence of predator-induced density-dependent mortality in marine reef fish populations (Anderson 1993, Forrester 1995, Tupper and Boutilier 1995, Hixon and Carr 1997, Steele 1997a, Caselle 1999, Schmitt and Holbrook 1999). These few studies of reef fishes reflect both the rarity with which predation events are observed in nature and the difficulty in manipulating both mobile predators and prey fish.

Here I explore the effects of a predator on rates of mortality of a temperate reef fish, the kelp perch (*Brachyistius frenatus*: Embiotocidae). I provide evidence that predation can cause spatial density dependence in local populations of kelp perch, and I identify the particular mechanisms underlying density-dependent mortality. Observational studies of the dynamics of local populations of kelp perch indicate that high spatial and temporal variation in the abundance of juveniles does not translate into similarly high variation in the abundance of adults, and that there is no direct correspondence in abundance within cohorts from the transition of juveniles to adults the following year (Anderson 1994). Such relationships are not unusual in the cohort development of fish populations (DeAngelis and Gross 1992, Chambers and Trippel 1997), but they can suggest that density-dependent processes may act to regulate local populations of this species. Direct evidence of density-dependent mortality is necessary to evaluate the potential for population regulation (Hixon 1998).

In this study, I first determined experimentally the per capita (proportional) mortality rates of juvenile kelp perch across a range of densities, caused by the behavioral responses of a piscivore, the kelp bass (*Paralabrax clathratus*: Serranidae). I then examined whether such rates were density dependent and assessed observationally at a larger spatial scale whether predation could be an important process regulating local populations of the kelp perch. Specifically, I asked four questions: (1) What is the per capita mortality rate of juvenile kelp perch caused by the functional response of kelp bass? (2) Does the presence and quantity of habitat structure provided by the giant kelp (*Macrocystis pyrifera*) alter this rate? (3) What are the separate and combined effects (and thus the relative importance) of the functional and aggregative responses by kelp bass on per capita mortality of juvenile kelp perch? (4) Does the relationship between the distribution and abundance of kelp perch and kelp bass at larger spatial scales suggest that predation has regulatory importance in the population dynamics of kelp perch?

METHODS

Natural history and study system

The kelp perch is a viviparous surfperch that commonly inhabits temperate reefs off the coast of southern California. Its abundance and distribution are closely tied to temporally and spatially variable stands of *Macrocystis pyrifera* (Bray and Ebeling 1975, Coyer 1979, Larson and DeMartini 1984, Carr 1989, DeMartini and Roberts 1990, Anderson 1994). After birth, young surfperch aggregate in groups at shallow depths immediately below the surface canopy of *M. pyrifera*, and both juveniles and adults maintain a close association with *M. pyrifera* and other kelps inhabiting rocky reefs (Anderson 1994). Unlike almost all other marine teleosts,

surfperches do not undergo planktonic dispersal as eggs or larvae; instead young surfperch are born of relatively large size essentially as miniatures of adults and continue to occupy the general habitat in which they were born. The kelp perch matures within one year of birth (Baltz 1984), lives for only 2–3 yr (Hubbs and Hubbs 1954), and has relatively high fecundity among surfperches (Baltz 1984), so that changes in the demography of young fish in their first year of life should soon be manifested within the adult population. Moreover, because of these life history characteristics and because local populations of kelp perch are relatively “closed” rather than “open” (Caswell 1978), any density dependence in demographic rates would be important at relatively small spatial scales.

The kelp bass is an abundant, ubiquitous predator of surfperches and many other fishes (Quast 1968, Love and Ebeling 1978, Ebeling and Laur 1985, Schmitt and Holbrook 1985, Holbrook and Schmitt 1988, Carr 1991, Steele 1997a, b) in kelp-forested reefs in southern California. At Santa Catalina Island, it is the most important predator of reef fishes because of its high numbers (also see Carr 1991, Steele 1997a, b).

All laboratory and field studies were conducted at the University of Southern California’s Wrigley Marine Science Center, Santa Catalina Island, California, USA (33°27' N, 118°29' W). Field experiments were performed within Big Fisherman Cove, an area of sand bottom bounded by rocky reefs dominated in cover by the understory alga *Sargassum palmeri* and stands of *Macrocystis pyrifera*. Observational relationships between the abundances of kelp perch and kelp bass at a larger spatial scale were examined at several reefs spanning a 12-km distance along the northeast leeward side of Santa Catalina Island.

Functional response: kelp perch density and habitat structure

I estimated proportional mortality over a range of densities of young kelp perch in the presence of kelp bass and differing amounts of *Macrocystis pyrifera* as habitat structure that provided possible prey refuges. Laboratory experiments were conducted during the summers of 1990 and 1991 to determine mortality rates of kelp perch caused by the functional response of the kelp bass. The densities of kelp perch used in experimental trials (10, 20, 40, and 60 fish per 5000-L pool; 5-m² bottom area) were within the natural range observed on reefs (Anderson 1993). Eight replicate trials were conducted for each treatment combination of four levels of kelp perch density and three levels of habitat structure, and six replicate trials were conducted for each prey density in the absence of habitat structure. Juvenile kelp perch were collected from reefs using SCUBA and BINCKE (benthic ichthyofauna net for coral-kelp environments) nets (see Anderson and Carr 1998). BINCKE nets were constructed of knotless nylon netting (6-mm mesh) attached to hinged frames of

PVC. A net was opened and swept upward in the upper water column by a single diver, collecting juvenile fish in the surface kelp canopy. Fish were selected haphazardly for each experimental trial from a 1700-L pool that was continually restocked with 200–400 fish (33–55 mm standard length [SL]). Kelp bass (18.5–30 cm SL) were collected by hook and line; this size range represented most kelp bass on reefs in the area. I used two kelp bass in every trial for each combination of habitat structure and density of kelp perch to ensure that at least one of these predators fed during a trial. One smaller kelp bass (18.5–24 cm SL) and one of larger size (25–30 cm SL) were paired together to minimize any differences in foraging rates dependent upon predator size. Moreover, to achieve similar levels of hunger and gut fullness, kelp bass remained unfed for 60 h prior to each trial. To further remove potential differences in individual predator foraging efficiency, six pairs of kelp bass were rotated among all levels of fish density and habitat structure. Habitat structure consisted of bundles of *M. pyrifera*, each composed of eight 2-m length fronds, which simulated both the floating surface canopy and upper vertically oriented fronds of *M. pyrifera*. Bundles of fronds were weighed to the nearest 0.1 kg wet biomass and distributed among pools to obtain equivalent amounts of biomass for a given level of habitat structure. One, two, and four bundles of fronds per pool corresponded to “low” (5.8–6.4 kg), “medium” (9.9–13.2 kg), and “high” (21.9–26.1 kg) levels of kelp biomass, respectively.

For a single experimental trial, each of two levels of the density of kelp perch were placed in a 5000-L circular pool with a given level of habitat structure. Both kelp perch and kelp bass were placed in the pools 2–6 h before beginning a trial; each pair of predators was restricted to a 12-mm mesh plastic cylinder (0.3 m diameter × 1.5 m length) that was lifted from the pool for their release at the appropriate time. Trials were run for 15 h beginning between 1700–1800, covering both dusk and dawn crepuscular periods when kelp bass forage most actively (Hobson et al. 1981). After this period, the number of kelp perch remaining in each pool was counted to determine the number of fish consumed, from which proportional mortality was calculated.

Aggregative response and predation intensity

To determine whether kelp bass exhibit an aggregative response to variable densities of kelp perch, I conducted a field experiment from 31 July to 14 August 1991. I enclosed four plots on a sandy bottom within Big Fisherman Cove. Each plot was surrounded by a 4 m diameter, 6-mm nylon mesh circular pen buoyed at the sea surface and anchored to the bottom (5–7 m depth). The volume within each pen was ~60 m³. Plots were separated spatially from each other and from a nearby reef by at least 12 m, a distance that generally exceeded the limits of underwater horizontal visibility

in this area. To provide habitat for juvenile kelp perch, 20 individual *Macrocystis pyrifera* were collected from nearby reefs, placed in nylon mesh bags, and weighed to the nearest 0.5 kg. Individual *M. pyrifera* were then ranked by biomass, and four *M. pyrifera* were anchored within each plot (95–105 kg/plot) to achieve similar amounts of biomass and physical structure among plots.

For each trial, the same numbers of kelp perch (10, 20, 40, and 60 fish) used in the laboratory were each assigned randomly to one of the four plots. As in the laboratory, juvenile fish were assigned haphazardly to each density level from a pool of 200–400 individuals (39–72 mm SL). To account for differences in the spatial location of plots, each level of the density of kelp perch was represented at least once in each plot. Kelp perch were placed within pens for 4–5 h before beginning a trial. At 1700–1800, the nylon mesh pens surrounding the plots were collapsed downward and secured to the bottom, allowing kelp bass complete access to the plots for 2 h, encompassing the dusk crepuscular period. At 5-min intervals, an observer on SCUBA stationed at each plot recorded the number and location (beneath the surface kelp canopy vs. open water column below) of both kelp perch and kelp bass. The number of kelp bass and the number of attempts at capturing kelp perch (“strikes”) were also tallied at 5-min intervals as estimates for a potential aggregative response and as a measure of predation intensity, respectively. Direct observation of plots over the 2-h period when kelp perch were exposed to kelp bass averaged 62% of the total time. At the end of 2 h, all kelp bass were chased from plots, whereupon the pens were pulled upward to the sea surface. The number of kelp perch remaining on each plot were collected the next morning to determine proportional mortality.

Losses unrelated to predation.—Two potential sources of losses of kelp perch that could not be attributed to predation were mortality from other causes (e.g., handling stress) while in the pens, and emigration from plots during the period that they were exposed to predators. Nonpredatory losses could contribute to or alter observed patterns of mortality attributed to predation, especially if loss rates were density dependent.

I investigated the extent of mortality of kelp perch due to causes unrelated to predation or emigration by conducting two trials in exactly the same way as described above, with the exception that pens were left in place and not collapsed downward. In each trial, the four levels of kelp perch density were allocated randomly to plots at the time that fish were normally placed within pens. The next morning, fish were removed from plots and counted to calculate mortality.

To assess the importance of emigration from experimental plots, I constructed a fifth plot of *Macrocystis pyrifera* that was surrounded by a 6-mm mesh pen identical to the other pens surrounding the four plots used in field predation trials. An additional pen of 18-mm

mesh, dyed green to reduce its visibility, was placed along the inside perimeter of the 6-mm mesh pen. On each of four days, kelp perch of the same numbers used in the predation trials were released onto the plot. Beginning at 1700–1800, the outer pen was collapsed downward and secured to the bottom, leaving the larger mesh pen intact. This procedure was done to effectively decouple predator-induced mortality from losses of kelp perch by emigration. Kelp perch could swim through the larger mesh pen, but only small kelp bass (<10–11 cm SL) were able to enter the plot. After collapsing the outer pen, emigration was monitored for 2 h, the same period of time allocated for a predation trial. After this period, the outer pen was pulled upward to the sea surface. Losses of kelp perch were then determined from the number of fish collected the next morning. The stomach contents of small kelp bass captured inside the pen were examined to determine whether they consumed any kelp perch.

Patterns at larger spatial scales

To determine if patterns of proportional mortality determined experimentally at a small spatial scale would “scale-up” to larger areas, I performed a series of surveys over a 4-yr period. If predation reduced prey population size and was an important factor leading to population regulation, one could expect an inverse relationship between predator and prey abundances (Taylor 1984, Hixon 1991, Hixon and Beets 1993). To determine whether the densities of kelp bass and kelp perch were negatively correlated among reefs, visual transects were conducted at 9–12 reefs surveyed annually from 1989 through 1992 (for methods see Anderson 1994). I recorded the number of juvenile kelp perch and of kelp bass >15 cm SL (approximately the minimum size at which kelp bass could consume kelp perch).

Recording the distribution of both kelp bass and kelp perch during the daytime vs. during crepuscular periods when kelp bass forage actively could lend additional circumstantial evidence (sensu Hixon 1991) to support predation as a factor regulating local populations. The diel distributions of kelp bass and kelp perch were censused on each of 6 d between 27 June and 9 July 1991 at Parson’s Landing, the only reef during the summers of 1991 and 1992 that supported a large stand of *Macrocystis pyrifera* with an area of continuous kelp surface canopy and high numbers of kelp perch. On each day, four 2 m wide × 2 m high × 30 m long transects were performed under the surface canopy of *M. pyrifera* (0–2 m depth) and at mid-water (~8–10 m, half the distance between the surface canopy and reef bottom) during the afternoon (1435–1630) and at dusk (1850–1950). The densities of both species from each period and depth stratum were examined to determine if kelp bass tracked the diel movements of kelp perch. Because young kelp perch also form aggregations, the group size of kelp perch was recorded during daytime

and dusk periods as a potential response to predator abundance.

Data analyses

Statistical analyses were performed using PC SAS version 6.03 software (SAS Institute 1988). I used linear regression to determine the relationship between the density of kelp perch and proportional mortality in laboratory pools as determined by the functional response for each level of habitat structure. Mortality values were transformed (arcsine square-root transformation) to meet assumptions of linearity and homogeneity of variances. I then employed analysis of covariance to determine if mortality rates differed significantly between levels of habitat structure, using the density of kelp perch as a covariate. Because the slopes of the regression lines for each treatment of habitat structure were not equal, I used the Johnson-Neyman technique (Wilcox 1987; see Huitema 1980) to determine differences among slopes within the range of covariate values. Because of potential differences in the size of juvenile kelp perch used in laboratory trials, I applied a two-factor analysis of variance (ANOVA) to determine if the mean lengths of juveniles used in pools were significantly different between levels of habitat structure or fish density. Shapiro-Wilk (Zar 1984) and Cochran's *C* (Winer 1971) tests were used to examine whether these data met assumptions of normality and homogeneity of variances; values were transformed if necessary, whereupon the assumptions were met.

I determined the shape of the functional response (consumption rate vs. density of kelp perch) in laboratory trials for each level of habitat structure using logistic regression of the relationship between the density of kelp perch and proportional mortality (see Juliano 1993). I examined the signs (positive or negative) of the linear and quadratic parameters to differentiate Type II from Type III functional responses (CATMOD procedure; SAS Institute 1988). I then applied nonlinear regression (NLIN procedure; SAS Institute 1988) to determine the significance and fit of the indicated nonlinear model and compared the coefficient of determination (r^2) with that of a linear model.

For the field experiment, I used linear regression to examine the relationship between the density of kelp perch and proportional mortality. Mortality values did not require transformation as determined by plotting predicted vs. actual values of mortality and residuals vs. the density of kelp perch. Regression was also used to explore the relationships between the density of kelp perch and the total number of strikes observed (predation intensity), the mean number of kelp bass observed (aggregative response), and a "calculated" per predator strike rate (a proxy for the functional response) by kelp bass at kelp perch (total strikes/mean number of kelp bass). The values for both mean number of kelp bass and strike rate were \log_{10} -transformed to meet the assumption of homogeneity of variances for

linear regression. For the calculated strike rate, I fit the data to a Type II functional response model and to a linear model to determine the best fit. Finally, a one-factor ANOVA was used to determine if there were significant differences in the mean size of kelp perch used for each level of density of fish placed on plots.

For comparisons of kelp perch and kelp bass abundance at larger scales, I used correlation to test whether there was a significant inverse relationship between the densities of kelp perch and kelp bass on reefs that could be expected if predator-induced patterns of density-dependent mortality occurred at larger spatial scales. I examined the diel distribution of kelp perch and kelp bass qualitatively, because observations were conducted when only one reef in the area had an appreciable stand of *Macrocystis pyrifera* and sufficient numbers of kelp perch; lack of replication prevented quantitative analysis.

RESULTS

Functional response and per capita mortality

In laboratory trials, proportional mortality in the absence of habitat structure showed an inversely density-dependent relationship (Fig. 1a; $r^2 = 0.31$; $F_{1,22} = 11.3$; $P = 0.003$). However, this relationship changed when a substantial amount of *Macrocystis pyrifera* habitat was placed into pools. A significant, negative relationship between proportional mortality and the density of kelp perch was also found when habitat structure was low (Fig. 1b; $r^2 = 0.42$; $F_{1,30} = 23.4$; $P = 0.0001$), but not when medium (Fig. 1c; $r^2 = 0.051$; $F_{1,30} = 2.65$; $P = 0.11$) or high (Fig. 1d; $r^2 = 0.0002$; $F_{1,30} = 0.006$; $P = 0.94$). Analysis of covariance revealed an interaction between the amount of *M. pyrifera* and the density of kelp perch ($F_{3,112} = 3.44$; $P = 0.02$), indicating that the relationship between the density of kelp perch and proportional mortality differed according to the amount of habitat structure. The Johnson-Neyman technique revealed that proportional mortality did not differ between the absence of and low amounts of *M. pyrifera*. Slopes did differ, however, between the absence of and a medium amount of *M. pyrifera* and between medium and high amounts of *M. pyrifera*. Differences in the slopes of these regression lines were a result of lower proportional mortality at lower densities of kelp perch in the presence of greater amounts of *M. pyrifera*, while higher densities of kelp perch experienced similar low rates of proportional mortality regardless of the amount of habitat structure, possibly due to predator saturation (maximum of ~six prey fish eaten per predator; Fig. 2).

Expectedly, the functional response of kelp bass showed a general increase in the number of kelp perch consumed per predator with an increase in the density of kelp perch (Fig. 2). Logistic regression analysis indicated that the relationship between consumption rate and the density of kelp perch was best described by a Type II functional response. For "none" (Fig. 2a; r^2

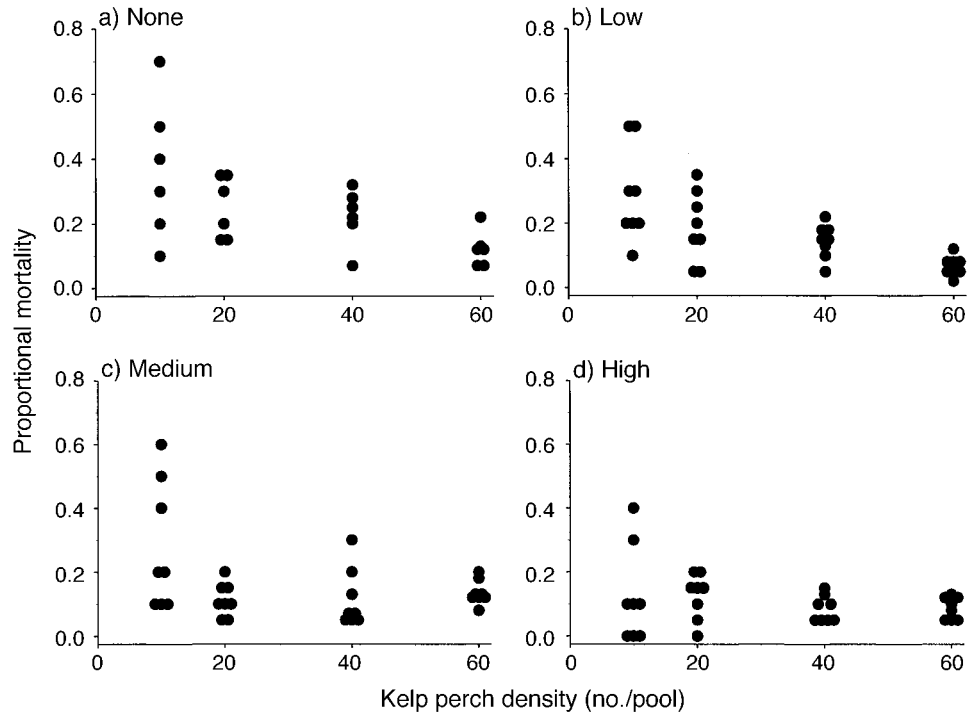


FIG. 1. Relationship between the density of kelp perch (no. individuals per pool) and proportional mortality under conditions of (a) none, (b) low, (c) medium, and (d) high amounts of habitat structure (giant kelp, *Macrocystis pyrifera*).

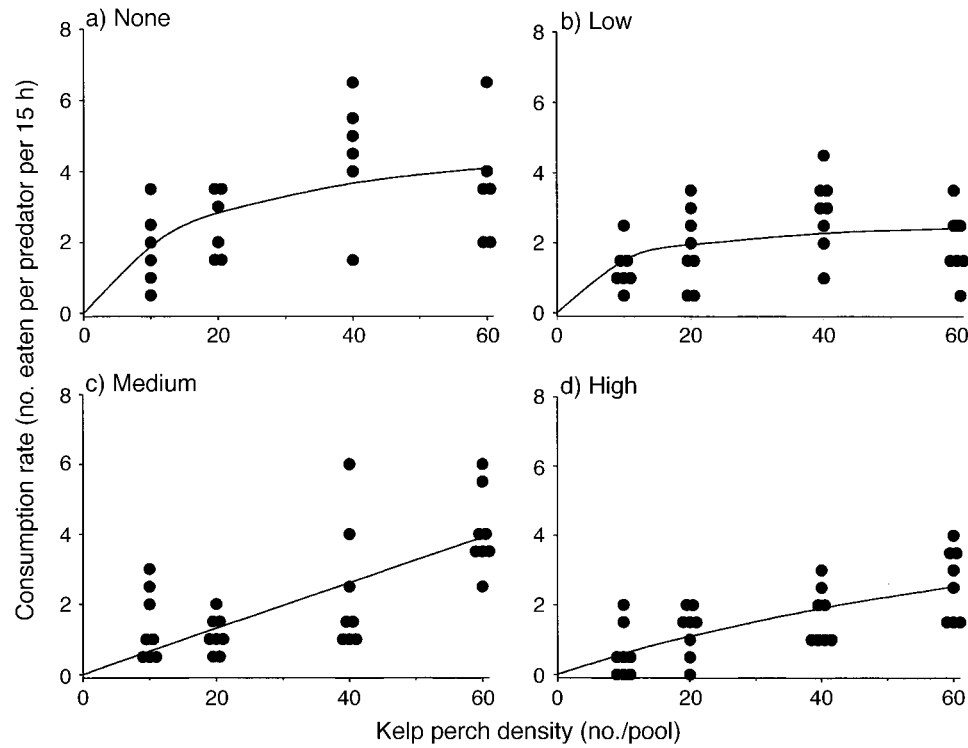


FIG. 2. Functional response of kelp bass (consumption rate vs. density of kelp perch) in laboratory pools among (a) none, (b) low, (c) medium, and (d) high levels of habitat structure (giant kelp, *Macrocystis pyrifera*).

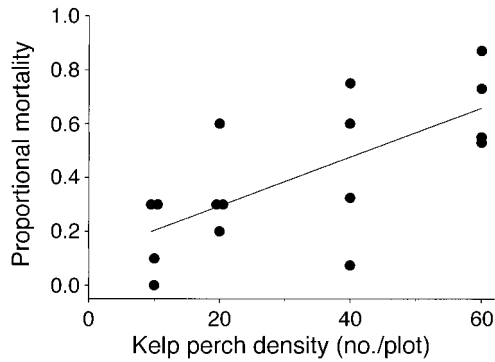


FIG. 3. Relationship between the density of kelp perch exposed to natural levels of kelp bass in the field and proportional mortality.

= 0.28; $F_{1,22} = 8.49$; $P = 0.008$), low (Fig. 2b; $r^2 = 0.12$; $F_{1,30} = 3.95$; $P = 0.056$), and medium (Fig. 2c; $r^2 = 0.52$; $F_{1,30} = 32.7$; $P < 0.001$) amounts of habitat structure, the Type II functional response had a better fit than linear models with $r^2 = 0.23$, $r^2 = 0.067$, and $r^2 = 0.46$ for increasing levels of structure, respectively. For the highest amount of habitat structure, the sign of the linear parameter was positive and the quadratic parameter negative, suggesting a Type III functional response. However, a Type II functional response had a slightly better fit (Fig. 2b; $r^2 = 0.47$; $F_{1,30} = 26.4$; $P < 0.001$) than a Type III functional response ($r^2 = 0.45$) or a linear model ($r^2 = 0.46$). With greater amounts of habitat structure, the functional response flattened out over the range of density of kelp perch.

The mean size of kelp perch used in laboratory trials differed among levels of habitat structure but not with the density of kelp perch (two-factor ANOVA: habitat structure, $F_{3,104} = 115.4$, $P = 0.0001$; fish density, $F_{3,104} = 1.32$, $P = 0.32$). A multiple comparison test (REGWQ option, GLM procedure; SAS Institute 1988) revealed significant differences in the size of kelp perch (measured before each trial) among all levels of habitat structure (low [56.1 ± 0.39 mm] > none [49.6 ± 0.30 mm] > high [46.5 ± 0.17 mm] > medium [41.9 ± 0.71 mm] amounts of *Macrocystis pyrifera*). However, because higher proportional mortality occurred in the absence or with lower amounts of *M. pyrifera*, patterns of mortality were not confounded by these differences in size.

Effects of functional and aggregative responses on per capita mortality

Opposite the pattern found in laboratory trials, proportional mortality in the field increased with higher densities of kelp perch (Fig. 3; $r^2 = 0.44$; $F_{1,14} = 13.0$; $P = 0.003$), indicating density-dependent mortality. Mortality of kelp perch among density levels was not confounded by the size of kelp perch used in the experiment (one-factor ANOVA; $F_{3,12} = 0.09$; $P = 0.97$). The strike rate by kelp bass at kelp perch, standardized to 10-min intervals, was positively related to the den-

sity of kelp perch (Fig. 4a; $r^2 = 0.43$; $F_{1,14} = 12.458$; $P = 0.003$), as was the mean number of kelp bass recorded on plots at 5-min intervals (Fig. 4b; $r^2 = 0.30$; $F_{1,14} = 7.29$; $P = 0.017$), suggesting an aggregative response. I calculated a "functional response" by dividing the total strike rate of all kelp bass (Fig. 4a) by the mean number of kelp bass (Fig. 4b) recorded at each density of kelp perch, with the assumption that strike rate was proportional to capture success across the range in density of kelp perch. There was a positive relationship, better fit by a Type II functional response curve (Fig. 4c; $r^2 = 0.42$; $F_{1,14} = 9.93$; $P = 0.007$) than by a linear model ($r^2 = 0.40$), between the strike rate per predator and the density of kelp perch, indicating that the consumption rate of kelp bass increased with higher densities of kelp perch.

Behavioral responses.—Observations of plots at 5-min intervals during field trials showed that the distribution of kelp perch and kelp bass over time shifted toward an increase in the proportion of fish just beneath the surface canopy of *Macrocystis pyrifera* (Fig. 5). Moreover, qualitative differences observed in the behavior of kelp perch changed with their density. Many fish at higher initial densities (40 or 60 fish) tended to

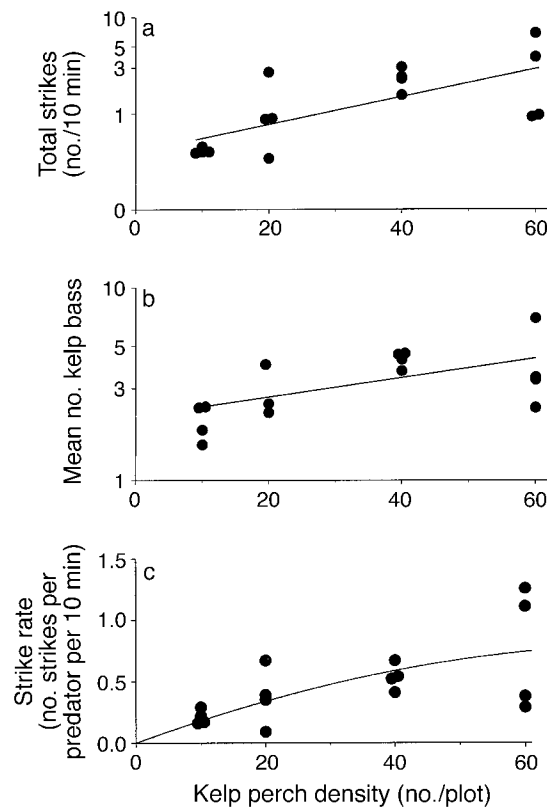


FIG. 4. Relationship between the density of kelp perch and (a) the total number of strikes by kelp bass at kelp perch, standardized to a 10-min interval, (b) the mean number of kelp bass recorded on field plots, and (c) the calculated per-predator strike rate.

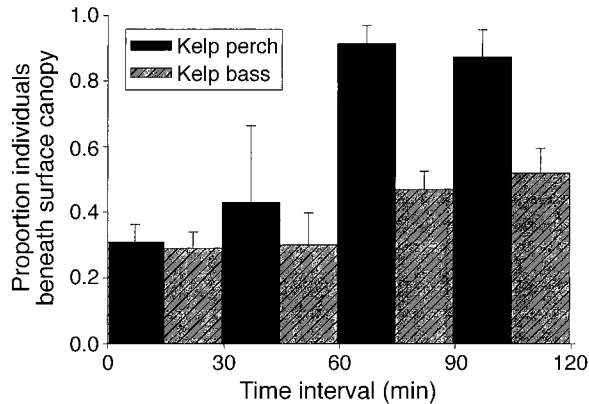


FIG. 5. Mean proportion of number of kelp perch and kelp bass that occurred beneath the surface kelp canopy vs. the water column below at 30-min intervals. Vertical lines indicate + 1 SE of observations at plots ($n = 16$).

congregate closely together in an aggregation beneath the surface canopy in the presence of kelp bass, while fish at lower densities (10 or 20 fish) usually disappeared into the uppermost fronds of *M. pyrifera* at the water surface.

Losses unrelated to predation.—There was no evidence that either emigration or other nonpredatory sources of mortality could account for the observed density dependence. In control trials where fish were placed in pens but not subjected to predators, mortality was trivial and independent of the density of kelp perch (Table 1), indicating that neither stress from handling nor other conditions contributed to mortality. In emigration trials, kelp perch passed easily through the large-mesh pen and would venture a few meters away before eventually returning to the plot. Emigration was minimal regardless of the density of kelp perch (Table 1). The greatest proportional loss of kelp perch was 15% (3 of 20 fish) but most losses were negligible. The few small kelp bass that entered the plot through the large-mesh pen could have contributed to losses of kelp perch that were presumed to have emigrated. From one to eight small kelp bass were collected from a plot after each emigration trial was completed, but a total of only two kelp perch were ever found in stomach contents. However, these data do not account for kelp bass that may have entered the plot, consumed kelp perch, and then departed.

Evidence for predation at larger spatial scales

Changes in the diel distribution of kelp perch and kelp bass were similar. The densities of both species almost doubled in the surface canopy of *Macrocystis pyrifera* at dusk (Fig. 6a, b). At that time, juveniles occurred immediately below the surface canopy, often within 0.5 m depth. In addition, the mean number of kelp perch in an aggregation at twilight was threefold that recorded in the afternoon (Fig. 7c). In examining the relative abundances of kelp perch and kelp bass

>15 cm SL among reefs, surveys during the 4-yr period revealed an inverse relationship between the densities of predator and prey (Fig. 8; $r = -0.38$; $P = 0.016$).

DISCUSSION

Two main types of field experimental evidence on the effects of predation on the abundance of reef fishes have been explored: (1) manipulation of refuge availability (Shulman 1984, 1985, Ebeling and Laur 1985, Behrens 1987, Hixon and Beets 1989, 1993, Caley and St. John 1996), and (2) manipulation of the presence of piscivores (Doherty and Sale 1985, Carr 1991, Caley 1993, Carr and Hixon 1995, Connell 1997, Hixon and Carr 1997, Steele 1997b). Both lines of evidence have suggested that predation can influence reef fish abundance (and consequently community structure), primarily through effects on mortality of young fish shortly after settlement from the plankton to reefs. In very

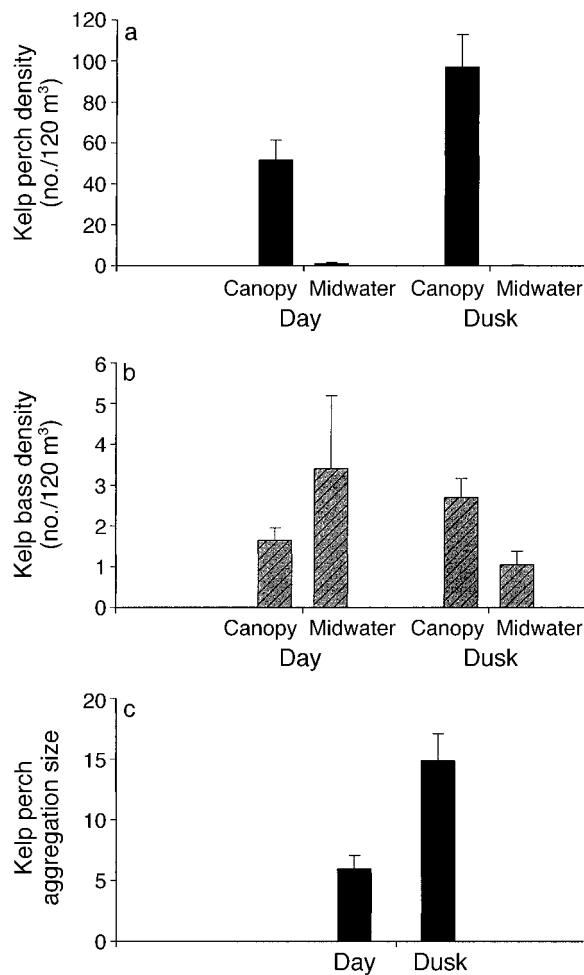


FIG. 6. Diel distribution of kelp perch and kelp bass in canopy and midwater depth strata at Parson's Landing Reef. Data are means and standard errors from four surveys: (a) the density of kelp perch, (b) the density of kelp bass, and (c) kelp perch aggregation size.

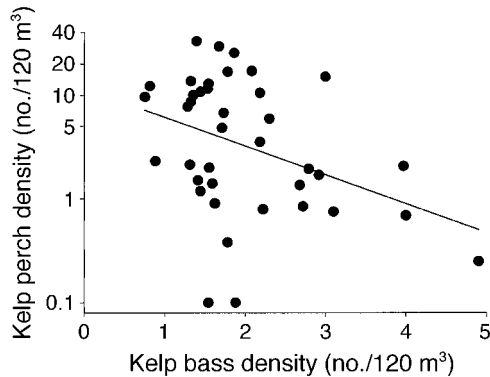


FIG. 7. The relationship between the density of kelp bass and kelp perch at reefs surveyed during 1989–1992 ($n = 39$).

recent studies (Forrester 1995, Tupper and Boutlier 1995, Hixon and Carr 1997, Steele 1997b, Caselle 1999, Schmitt and Holbrook 1999), manipulations of the density of resident reef fishes have resulted in density-dependent mortality and potential regulation of local populations. However, although density dependence has been detected, there is a need to identify and quantify the particular mechanisms involved.

Prey density, predator response, and habitat structure

In this study, I manipulated the density of juvenile kelp perch and examined both per capita mortality of kelp perch and the behavioral responses of its predator. Thus, I was able to determine both the existence and strength of density-dependent mortality and the causal mechanisms underlying such density dependence. Opposite patterns of proportional mortality were found between laboratory and field experiments in manipulations of the density of kelp perch. Proportional mortality within laboratory pools decreased with increasing densities of kelp perch (inverse density dependence) in the presence of a constant, low number of kelp bass and little or no habitat structure, indicative of a Type II functional response (Holling 1959). However, with greater amounts of *M. pyrifera*, mortality rates decreased and were ultimately similar across all densities of kelp perch (i.e., density independent); the structure of *M. pyrifera* apparently hampered foraging by the kelp bass, at least at lower densities of kelp perch. This result suggested an alteration of the functional response, because consumption rates decreased at lower densities of kelp perch but continued to increase at higher densities of fish under conditions of medium and high amounts of *M. pyrifera* (Fig. 2). One explanation for such a shift in the functional response was the existence of a prey refuge provided by the physical structure of *M. pyrifera*.

The mortality of kelp perch when exposed to natural levels of predation by kelp bass was strongly density dependent. Equivalent amounts of *Macrocystis pyrifera*

TABLE 1. Losses of juvenile kelp perch from emigration and from other nonpredatory sources of mortality.

Fish density	Emigration	Other sources of mortality
10	0	0.05 (0.05)
20	0.15	0.08 (0.025)
40	0.05	0
60	0.02	0.02 (0.025)

Notes: Values for each level of fish density are the proportions of individuals not recovered from the total number introduced to a plot. Numbers in parentheses indicate 1 SE of two trials conducted for each level of density.

among plots might have contributed to density-dependent mortality because per capita refuge availability would necessarily decline with an increase in the density of kelp perch. The behavior of juvenile kelp perch in response to the presence of kelp bass was also density dependent. At low densities, kelp perch sought the cover of the uppermost fronds of *M. pyrifera*, whereas at high densities, a large proportion of fish congregated in the upper water column of the plot beneath or adjacent to the surface kelp canopy. These different behaviors were consistent with density-dependent anti-predator behaviors observed for pollock (*Pollachius virens*), which associate with macroalgae when confronted with an avian predator model (Rangeley and Kramer 1998).

Many stands of *Macrocystis pyrifera* are small isolates of habitat. However, it is possible that the rates of mortality of kelp perch observed in this field experiment may have been higher than that occurring on

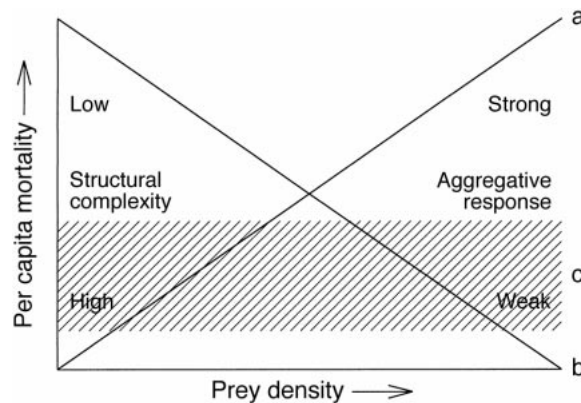


FIG. 8. Conceptual model of differential patterns of mortality for local populations of kelp perch dependent upon the degree of habitat structural complexity at lower densities of kelp perch and the strength of an aggregative response by kelp bass at higher densities of kelp perch: (a) density-dependent mortality with high structural complexity and a strong aggregative response, (b) inverse density-dependent mortality with low structural complexity and a weak aggregative response, and (c) density-independent mortality (shaded region) caused by medium to high levels of structural complexity and a relatively weak aggregative response.

reefs of much greater area with large stands of *M. pyrifera* because small habitat isolates may have been more attractive to kelp bass. Even so, the aim of this study was to examine relative rates of mortality across densities of kelp perch, a valid approach to examine the potential for density-dependent mortality and population regulation (Hixon 1998).

The relative importance of the functional response and an aggregative response as mechanisms causing density-dependent mortality seems clear. The positive relationship between the density of kelp perch and the number of kelp bass reveals an aggregative response by kelp bass. The pattern of inverse density-dependent to density-independent mortality observed in laboratory trials with Type II functional responses and the functional response calculated from field trials (also Type II) strongly suggests that the aggregative response of the kelp bass is the primary cause of predator-induced, density-dependent mortality. Density-dependent mortality from behavioral responses of predators can be caused in only two ways (Hassell 1978): either (1) the presence of a sigmoidal Type III functional response alone, or (2) the presence of a Type II functional response and an aggregative response. Thus in this study, the aggregative response is primarily responsible for the observed pattern of density-dependent mortality.

The functional response of a predator to varying densities of prey has been quantified in several studies, most commonly for parasitoids and other terrestrial arthropods (see Murdoch and Oaten 1975, Hassell 1978), whereas the effects of an aggregative response have been examined less frequently (Hassell and May 1974, Murdoch and Stewart-Oaten 1989, Wrona and Dixon 1991). Turchin and Kareiva (1989) found that aphids (*Aphis varians*) forming large colonies experienced less predation risk, even though predatory lady beetles (*Hippodamia convergens*) exhibited an aggregative response. Apparently, the rate of increase in the size of these colonies swamped the consumption rate of the number of beetles attracted to them. In an investigation of the predator-prey relationship between two estuarine fishes, Wright et al. (1993) manipulated the density of predatory southern flounder (*Paralichthys lethostigma*) in ponds. They observed that mortality rates of spot (*Leiostomus xanthurus*) were higher than expected given a linear increase in predator density. This result suggested that individual foraging rates of flounder increased at higher densities, presumably due to a strong functional response.

The above two examples underscore the need to address both the functional and aggregative responses of predators in evaluating the mechanisms underlying predator-induced, density-dependent mortality. The experiments I have conducted in this study illustrate how the strength of these predatory responses can generate different patterns of mortality with prey density and different interpretations of predation risk. In evaluating

only the functional response of kelp bass to kelp perch, the patterns of inverse density-dependent to density-independent mortality would lead one to conclude that predation does not have regulatory importance for local populations of kelp perch. By contrast, field trials provided strong evidence for predator-induced, density-dependent mortality and potential population regulation via the aggregative response by kelp bass. However, only evaluating the strength of both predatory responses can identify and determine the relative importance of the causal mechanisms of density-dependent mortality. This may be especially important in explaining differential effects of predation when there is variability in patterns of mortality; Booth (1995) found density-dependent survival of domino damselfish (*Dascyllus albisella*) present in one year but not the next, and Sano (1997) found density-dependent mortality in two years of a 3-yr study of the sand goby (*Sagamia geneionema*).

The manipulation of habitat structure in this study demonstrated that the amount of *M. pyrifera* lowers predation risk of juvenile kelp perch, suggesting that *M. pyrifera* may provide an effective refuge from predators. Macrophytes have reduced rates of predation of fishes in aquatic environments by impeding the foraging abilities of predators (reviewed by Heck and Crowder 1991). The structural complexity (e.g., density, biomass, surface area, morphology) of these macrophytes has played a major role in this regard (Savino and Stein 1982, Werner et al. 1983, Ebeling and Laur 1985, Holbrook and Schmitt 1988). In many studies, some "threshold" level of habitat complexity was necessary before predator foraging success was reduced significantly (see Gotceitas and Colgan 1989). For the kelp perch, a threshold amount of *M. pyrifera* canopy cover on reefs was critical for recruitment success of young (Anderson 1994). Because only reef-based processes could induce mortality in kelp perch (the vagaries of larval dispersal and supply are nonexistent for this species), predation appears to have played a significant role in the population dynamics of this species.

Circumstantial evidence for predation at larger spatial scales

The prediction of a negative relationship between predator and prey abundances, indicative of predation as an important process at larger spatial scales (Hixon 1991), was supported by censuses of kelp bass and kelp perch at several reefs over a four-year period. In addition, both kelp perch and kelp bass at Parson's Landing reef showed an increase in their densities just under the surface canopy at twilight when kelp bass foraged most actively, accompanied by a dramatic increase in the aggregation size of kelp perch. This circumstantial evidence supported the idea that predation could be an important process for local population dynamics of kelp perch at the scale of entire reefs.

The importance of scale in examining the processes affecting population dynamics (Schneider 1994) calls for linking experiments at small scales with observations at large scales (Doherty 1991, Hixon 1998). Because the kelp perch has relatively closed populations in which young are retained on the reef on which they were born, processes that affect population dynamics at small scales may also be more readily apparent at larger scales because local fecundity and recruitment success are strongly coupled.

Conclusions

Studies to date support the perception that predation is an important process in the dynamics of marine reef fish populations. However, before the mechanisms underlying these dynamics can be understood, the consequences of behavioral responses of predators to their prey must be examined. In this study, the interrelationships of the functional response, aggregative response, and habitat structure suggest a potentially stabilizing effect on local populations of kelp perch. A Type III functional response and an aggregative response both induce density-dependent mortality in prey and thus promote stability in populations (Murdoch and Oaten 1975, Hassell 1978), although compensatory mortality can result from either of these responses without the other (Hassell 1978). Here, the aggregative response appears to be responsible for predator-induced compensatory mortality. The structural complexity of *Macrocystis pyrifera* may contribute to this pattern by providing an effective refuge for juvenile kelp perch at lower densities. However, as illustrated by the opposite patterns of mortality found between laboratory and field experiments, the pattern of mortality expressed should be the result of an interaction between the strength of an aggregative response and the degree of structural complexity (density/biomass), which can result in inversely density-dependent, density-independent, or density-dependent mortality (Fig. 8). Taken together, the strength of the behavioral responses by kelp bass to kelp perch and the structural complexity of *M. pyrifera* can result in compensatory mortality in juvenile kelp perch, which in turn may result in the low spatial and temporal variation in the size of adult populations (Anderson 1994). Indeed, predation may be a driving force in regulating local populations of the kelp perch and possibly other reef fishes.

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