PREDATION, HABITAT COMPLEXITY, AND VARIATION IN DENSITY-DEPENDENT MORTALITY OF TEMPERATE REEF FISHES

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Abstract. Density dependence in demographic rates can strongly affect the dynamics of populations. However, the mechanisms generating density dependence (e.g., predation) are also dynamic processes and may be influenced by local conditions. Understanding the manner in which local habitat features affect the occurrence and/or strength of density dependence will increase our understanding of population dynamics in heterogeneous environments. In this study I conducted two separate field experiments to investigate how local predator density and habitat complexity affect the occurrence and form of density-dependent mortality of juvenile rockfishes (*Sebastes* spp.). I also used yearly censuses of rockfish populations on nearshore reefs throughout central California to evaluate mortality of juvenile rockfish at large spatial scales. Manipulations of predators (juvenile bocaccio, *S. paucispinus*) and prey (kelp, gopher, and black-and-yellow [KGB] rockfish, *Sebastes* spp.) demonstrated that increasing the density of predators altered their functional response and thus altered patterns of density dependence in mortality of their prey. At low densities of predators, the number of prey consumed per predator was a decelerating function, and mortality of prey was inversely density dependent. However, at high densities of predators, the number of prey killed per predator became an accelerating response, and prey mortality was directly density dependent.

Results of field experiments and large-scale surveys both indicated that the strength of density-dependent mortality may also be affected by the structural complexity of the habitat. In small-scale field experiments, increased habitat complexity increased the strength of density-dependent mortality. However, at large scales, increasing complexity resulted in a decrease in the strength of density dependence. I suggest that these differences resulted from scale-dependent changes in the predatory response that generated mortality. Whether increased habitat complexity leads to an increase or a decrease in the strength of density-dependent mortality may depend on how specific predatory responses (e.g., functional or aggregative) are altered by habitat complexity. Overall, the findings of this study suggest that rates of demographic density dependence and the resulting dynamics of local populations may largely depend upon attributes of the local habitat.

Key words: density dependence; functional response; habitat complexity; mortality; predation; predator facilitation; recruitment limitation; Sebastes.

INTRODUCTION

Population dynamics are driven by changes in demographic rates, and density-dependent rates are particularly important in regulating dynamics. For example, inverse (depensatory) density dependence can accelerate growth or decline in population numbers whereas direct (compensatory) density dependence can act to regulate populations and dampen fluctuations in population size (Murdoch 1994). Variation in the strength of density dependence can have many important ecological consequences, including those that affect the dynamics and viability of populations (e.g., Ginzburg et al. 1990), community structure (e.g., Emlen 1984), maintenance of species diversity (e.g., Connell

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1978), and detection of density dependence (Wilson and Osenberg 2002, Shima and Osenberg 2003). Because of the theoretical and practical importance of understanding density dependence, there is a need for more empirical studies that focus in detail on the mechanisms generating density dependence and how these mechanisms are likely to vary in space and time.

Predation is an important source of demographic density dependence and may contribute to population regulation (Murdoch and Oaten 1975, Taylor 1984, Cappuccino and Price 1995, Turchin 2003). Regulation often occurs through a numerical response of predators to the abundance of their prey (reviewed by Taylor [1984] and Turchin [2003]). However, many populations experience large fluctuations in recruitment that are not necessarily related to local population size. The regulation of these "open" populations may depend upon short-term, behavioral responses of predators (i.e., functional and aggregative) rather than long-term, numerical responses (Hixon et al. 2002). At relatively

PLATE 1. Predator and prey used in experimental manipulations. (Upper) Bocaccio rockfish (approximately 12 cm total length). Photo credit: D. Johnson. (Lower) Recently settled kelp rockfish (2 cm total length). Photo credit: A. Ammann.

prey (e.g., Karieva and Sahakian 1990) and may affect the long-term stability of predator–prey systems (Murdoch and Oaten 1975, Stenseth 1980, Sih et al. 1987). However, the effects of structural complexity and refuge space on predator–prey interactions may not always be straightforward (Lynch et al. 1998), and the role of structural complexity in mediating density-dependent predation needs to be evaluated further.

This study focused on predator–prey interactions in an assemblage of kelp forest fishes. I conducted two separate field experiments investigating the manner in which predator response and density-dependent mortality of juvenile rockfishes can be modified by (1) local predator density and (2) habitat complexity. I also investigated how patterns in mortality of juvenile rockfishes varied at large spatial scales (nearshore reefs throughout central California, USA) with a specific focus on how density-dependent mortality varied as a function of local predator density and habitat complexity.

METHODS

This study involved both field experiments and analyses of large-scale population dynamics. All experiments were conducted in Carmel Bay, central California, USA (36°33.6′ N, 121°56.3′ W) in the summer of 2003. Shallow, subtidal habitats in this area were dominated by rocky reefs that supported stands of giant kelp. Long-term monitoring surveys of rockfish populations were conducted on nearshore reefs throughout central California and ranged over 200 km of coastline, from southern Big Sur (35°31.9′ N, 121°05.3′ W) to northern Monterey Bay (36°58.5′ N, 122°09.1′ W).

In this study, prey species were juveniles of the "KGB" species complex, which includes kelp (see Plate 1), gopher, and black-and-yellow rockfish (*Sebastes atrovirens*, *S. carnatus*, and *S. chrysomelas*, respectively). As juveniles, these species are very similar in behavior and appearance, school together, and are difficult to differentiate in the field (Anderson 1983, Carr 1991). Common predators of these juvenile rockfish include young-of-the-year (YOY) bocaccio (*Sebastes paucispinus*; see Plate 1) and YOY olive rockfish (*S. serranoides*). Previous studies demonstrated that predation causes density-dependent mortality of juvenile rockfish and that density-dependent mortality was evident at the scale of nearshore reefs (kelp beds approximately 500 × 70 m in size; Johnson 2006).

Experiment 1: Predator density and functional response

To evaluate how local density of predators affects their functional response, I orthogonally manipulated predator (juvenile bocaccio 11–14 cm total length [TL]) and prey (juvenile KGB rockfish 1.5–3.0 cm TL) densities within enclosed units of habitat and measured prey mortality after a 48-hour period, hereafter referred to as a "trial." Habitat units ($n = 4$) were deployed in the field and were designed to mimic a large kelp plant. Each unit consisted of a standardized volume of kelp (three

short time scales, the impact of an average predator on its prey population will depend on the functional response of a predator (i.e., the number of prey killed per predator per unit time). Although understanding the functional response is crucial to understanding predator–prey interactions, functional responses have typically been described by simple models (e.g., Holling 1959). Criticism of simple functional response models (e.g., strictly prey-dependent models) has highlighted the potential for predator–predator interactions to alter predator response (Sih et al. 1998, Abrams and Ginzburg 2000). Indeed, empirical evidence suggests that although local density of predators is likely to affect their functional response, understanding the nature of predator–predator interactions and the resultant effect on prey survival requires more attention (e.g., prey risk may be reduced by predator interference or prey risk may be enhanced by predator facilitation; Artidi and Akcakaya 1990, Sih et al. 1998, Abrams and Ginzburg 2000).

Predator–prey interactions may also be modified by the availability of prey refuge space (Jeffries and Lawton 1984). Structurally complex habitats may provide refuge space for prey and/or reduce predator efficiency (Crowder and Cooper 1982, Savino and Stein 1982, Schneider 1984, Babbit and Tanner 1998). Such effects may determine how strongly predators regulate their

bundles of three 3 m long fronds with blades measuring 45–60 cm long and separated by 15–20 cm) attached to a $3 \times 2 \times 1.5$ m deep floating PVC frame that was enclosed by a 3.2-mm nylon mesh net that prohibited migration of predators or prey. Within enclosed habitats, three predator densities (1, 3, and 5 predators/enclosure) were crossed with eight prey densities (10, 15, 25, 30, 40, 50, 60, 70 prey/enclosure), and trials were repeated over time such that each combination of predator and prey density was replicated in two trials. Since both predator and prey species tend to be found in aggregations, the numbers used in this experiment were chosen based on group size rather than density per unit volume or area and are within the observed natural range (Appendix B).

For each trial, prey fish were allowed to acclimate in the enclosures for ~4 hours before predators were introduced. The species were then allowed to interact for 48 hours. At the end of each trial, all fish were removed from the enclosures and counted. I conducted four control trials with 35 prey and no predators. All 35 prey in each trial were still present after 48 hours, so I interpreted all loss of prey as mortality. To ensure similarity in hunger level, predators (which had often been feeding prior to collection) were kept in separate enclosures in the field for 96 hours prior to being used in experiments. Predators were used no more than twice in order to minimize effects of learned behavior.

For this type of experiment, the form of a predator's functional response can be determined by using logistic regression to analyze how the proportion of prey eaten changes as a function of the number of prey available (Trexler et al. 1988, Juliano 2001). This approach will identify any region of density-dependent prey mortality, and differences in the coefficient of the linear term in such regressions can be used to diagnose the form of the functional response (e.g., Type I, II, or III, sensu Holling [1959]). A negative coefficient for the effects of prey density on the proportion eaten indicates a saturated (e.g., Type II) response whereas a positive coefficient indicates an increasing (e.g., Type III) response (Juliano 2001). In my analysis I first tested for a difference in form of the functional response among the three predator densities. I used a logistic regression to analyze proportion of prey eaten as a function of three variables: the number of prey available, an indicator variable for predator density, and their interaction. Since the interaction term was significant (see *Results*), I analyzed regressions for each predator density separately to examine how the form of the functional response changed as predator density increased.

Experiment 2A: Habitat complexity and prey mortality

To examine how habitat complexity can affect the strength of density-dependent mortality of juvenile KGB rockfish, I manipulated both their abundance and the complexity of their habitat. This experiment was performed in a non-caged setting, and treatments were exposed to free predators. I conducted manipulations

TABLE 1. Manipulations of the number of fish and kelp stipes on habitats of standardized volume produced two different levels of habitat complexity (expressed as refuge-based densities of fish, i.e., number of fish per kelp stipe).

Treatment	No. fishes in group	No. kelp stipes	Refuge-based density
High complexity	18	9	2
	24	12	2
	30	15	2
	36	18	2
	42	21	2
	48	24	2
Low complexity	18	6	3
	24	8	3
	30	10	3
	36	12	3
	42	14	3
	48	16	3

Notes: Experiments compared loss as a function of fish number and habitat complexity. Number of replicates = 1 per cell. All experiments were conducted in Carmel Bay, central California, USA.

within replicate units of habitat that consisted of giant kelp attached to a floating $2 \times 1.5 \times 1$ m PVC frame. Units of kelp habitat were located ~12 m above a sand-bottom habitat and spaced 17 m from one another and 20 m from nearby reefs. I varied the number of fish per treatment (18, 24, 30, 36, 42, 48 fish/5-m^3 habitat unit) to measure density-dependent mortality and compared the rate of density dependence between two levels of habitat complexity. To maintain levels of habitat complexity and to avoid confounding refuge-based density (i.e., number of fish per unit kelp) with abundance-based density (i.e., number of fish per habitat unit), I added kelp fronds (3.3 m long with 45–60 cm blades and 15–20 cm between each blade) in constant proportion to the number of fish on each treatment, with low and high complexity represented by ratios of 3 and 2 fish/kelp frond, respectively (Table 1). Past experiments using the same units of habitat demonstrated that density-dependent loss only occurred on treatments exposed to predators (Johnson 2006). Consequently, all treatments were exposed to predators, and any density-dependent loss was interpreted as an effect of predation.

Fish were tagged with externally visible, subcutaneous injections of elastomer (Northwest Marine Technology, Shaw Island, Washington, USA), color-coded to identify the treatment into which each fish was placed. To minimize any effects of handling and tagging, I stocked each plot with tagged fish and began tracking the loss of fish from each plot only after the required density of fish remained for 24 hours. After this period I revisited plots every 1–2 days to identify and count the number of fish remaining. Any new recruits or migrants were removed as needed. Prey fish were not replaced. For each treatment, I calculated the daily per capita loss rate between each census as −(ln(number of fish present at time = $t + x$) − ln(number of fish present at time = t) ÷ x), where x = the number of days between censuses. This

TABLE 2. Output of logistic regression analyses used to determine the functional response of juvenile bocaccio rockfish (*Sebastes paucispinus*).

No. predators	Parameter	Value	SE	t	P
1	intercept	−1.491	0.363	−4.108	
	prey density	−0.019	0.00776	−2.448	0.015
3	intercept	−1.841	0.321	−5.74	
	prey density	0.00451	0.00613	0.736	0.46
5	intercept	−1.657	0.265	−6.254	
	prey density	0.0223	0.00498	4.474	0.0343†

Notes: For each predator density, the proportion of prey eaten was analyzed as a function of prey density. A negative coefficient for prey density indicates a decelerating (e.g., Type II) functional response, whereas a positive coefficient indicates an initially accelerating functional response (e.g., Type III). Significance values were calculated using a drop-in-deviance test, with standard error increased to adjust for extra-binomial variation when needed (marked by †).

measure was averaged over the 14-day experiment to estimate the mean daily mortality rate. I used an analysis of covariance to evaluate the effects of both fish density and habitat complexity on per capita loss rates.

Experiment 2B: Habitat complexity and emigration

Although previous experiments within this type of experimental array demonstrated that emigration of fish from habitat units was density independent when habitat was held constant (Johnson 2006), it was unknown whether emigration rates could vary with the amount of habitat in an experimental unit. As an additional control, I conducted a separate experiment in which I established plots with nine different densities of kelp (0, 6, 9, 12, 15, 18, 21, 24 fronds/5 m^3) and stocked each plot with 30 juvenile kelp rockfish (all 1.5–3 cm TL). All plots were caged with a 1.3-cm nylon mesh that excluded predators (as small as 7 cm TL) but allowed free movement of juvenile rockfish. This experiment also ran for 14 days, and loss rates were calculated as in experiment 2A, with loss interpreted as emigration.

Large-scale mortality patterns

To evaluate how predator density and habitat complexity affect the strength of density-dependent mortality of rockfishes at large spatial scales, I used yearly counts of rockfishes to analyze patterns in mortality during their first year in nearshore reef habitat. Visual transect surveys were conducted at sites throughout central California. Each site (~500 m alongshore by 70 m wide) was surveyed with a total of 24 transects that measured 30 × 2 × 2 m. Transects were randomly located within zones that were stratified by depth and alongshore distance, thus ensuring even coverage of the reef area. On each transect, divers identified, counted, and visually estimated the size of fishes. Divers also collected data on predator density (sum of all piscivorous fishes encountered on transects) and two measures of habitat complexity: substrate relief and kelp density (primarily *Macrocystis* plants that provide a large amount of three-dimensional structure). Substrate relief was recorded every 0.5 m along each transect and was measured as the vertical distance between the highest and lowest points

within a 1 × 0.5 m area. For analyses, substrate relief measurements were converted to a 1–4 numerical scale (1 = 0–0.1 m, 2 = >0.1–1 m, 3 = >1–2 m, 4 = >2 m) and averaged for each transect.

Large-scale patterns of mortality were analyzed for both the KGB species complex and blue rockfish (*Sebastes mystinus*), a common species that is representative of many rockfishes that recruit to temperate reefs and associate with hard substrate, as opposed to macroalgae. To determine mortality rates, I compared the abundance of recruits (defined as individuals <9 cm TL for blue rockfish and <7 cm TL for KGB) to the abundance of 1-yr-olds (10–14 cm TL for blue rockfish and 8–15 cm TL for KGB) at the same site in the next year. Although loss of juveniles could be caused by emigration, mortality, or both, I interpreted loss as mortality because there is ample evidence that rates of predation upon juvenile rockfishes are high (Hallacher and Roberts 1985, Adams and Howard 1996, Hobson et al. 2001), and evidence from substantial tagging studies suggests that the species I examined move very little as juveniles and are unlikely to emigrate from a kelp bed (Miller and Giebel 1973, Hoelzer 1988). I estimated instantaneous mortality rates by taking the difference between the natural $\log(x + 0.01)$ of the number of 1-yr-olds and the natural $\log(x + 0.01)$ of the recruits. Data were $\ln(x + 0.01)$ transformed to include several cases in which the number of 1-yr-old fish encountered on visual surveys was estimated as zero. The value of the constant added (0.01) was chosen because it approximated the smallest non-zero fish density recorded in these surveys (0.013 fish/120 m^3) and did not lead to excess skewness or kurtosis in the data (Berry 1987).

To evaluate both the independent and interactive effects of prey density, habitat complexity, and local predator density on mortality of juvenile rockfishes, I used multiple regression analyses with instantaneous mortality as the dependent variable. I included initial density of juveniles, predator density, substrate relief, kelp density, census year, and all possible interactions as predictor variables. In these analyses, factors that significantly interacted with density were interpreted as those that affect the strength of density-dependent
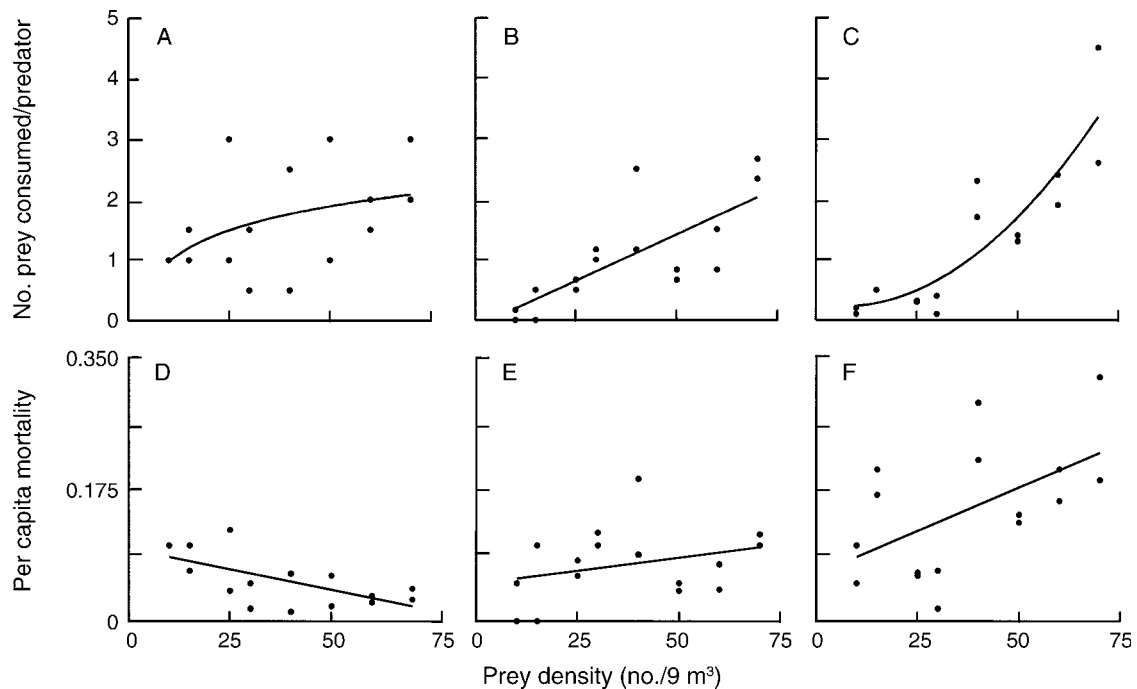
FIG. 1. (A–C) Functional response of predators and (D–F) per capita mortality of prey in predator–prey manipulation experiments. Per capita mortality was calculated as the proportion of prey killed at the end of each 48-hour trial. At low predator densities (1 predator/9 m³), functional response decelerated slightly as prey density increased (A) and resulted in prey mortality that was inversely density dependent (D). At intermediate predator densities (3 predators/9 m³), functional response appeared to be linear (B) and resulted in density-independent mortality of prey (E). At high predator densities (5 predators/9 m³), functional response was an accelerating, curvilinear function (C) and mortality of prey was directly density dependent (F). All experiments were conducted in Carmel Bay, central California, USA.

mortality. For both types of rockfish, I performed stepwise multiple regression analyses and selected best-fit models using Akaike's corrected Information Criterion (AIC_c).

I analyzed data collected from 14 sites over a period of four years. Not every site was sampled each year. In this analysis, I used observations of cohorts (year classes) at each site as independent data points even though some sites contributed multiple cohorts to the analysis (e.g., Beukers and Jones 1997, Shima 2001). This approach may confound spatial and temporal sources of variability in mortality. However, factors that may vary in time and space and that were likely to affect mortality (juvenile density, predator density, habitat complexity) were explicitly accounted for in this analysis. In addition, I included a term for census year in my analysis to account for any yearly variation in mortality that remained unexplained by other factors (e.g., yearly variation in oceanographic conditions).

RESULTS

Experiment 1: Predator density and functional response

Logistic regression analysis indicated that the relationship between the proportion of prey eaten and the density of prey significantly varied among predator densities (predator density × prey density interaction, $P = 0.005$). Further analysis indicated that with one predator per enclosure, the proportion of prey eaten significantly declined with number of prey available (Table 2). However, when predator density was increased to three per enclosure, proportion eaten did not significantly change with density (Table 2). Finally, when predator density was further increased to five per enclosure, the proportion of prey eaten significantly increased with the number of prey available (Table 2).

Patterns in the functional response of predators and resultant relationships between density and mortality of prey are illustrated in Fig. 1. In all cases, the number of prey consumed per predator increased as a function of prey density. However, at the lowest density of predators prey consumption was a decelerating function (Fig. 1A). As prey density increased, the number of prey killed became a smaller proportion, resulting in prey mortality that was inversely density dependent (Fig. 1D). At intermediate predator densities, the functional response was a linear increase (Fig. 1B). Although more prey were killed at high prey densities, this increase more or less tracked the increase in prey density, and the resultant mortality was independent of prey density (Fig. 1E). When predator densities were highest, the functional response became an accelerating
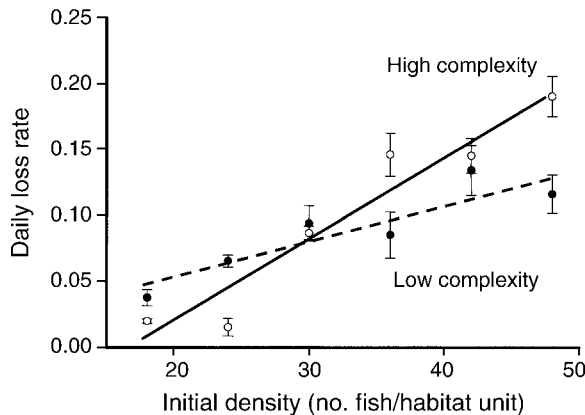
FIG. 2. Per capita loss (mean ± SE) as a function of initial number of fish on isolated units of habitat. Loss rates are expressed for both high (2 fish/kelp stipe) and low (3 fish/kelp stipe) levels of habitat complexity. Daily loss rates were averaged between each census and were calculated as $-(\ln[\text{number of fish present at time} = t + x] - \ln[\text{number of fish present at time} = t] \div x)$, where x is the number of days between censuses.

function (Fig. 1C). This accelerating consumption rate resulted in a higher proportion of prey killed at high densities, thereby causing density-dependent mortality (Fig. 1F).

Experiment 2: Habitat complexity and prey mortality

Experiment 2B assessed the effect of kelp density on per capita emigration rates. This experiment indicated that it was unlikely that the structure of the frame and cage provided suitable habitat for juvenile rockfish, since fish never remained on a caged frame with no attached kelp stipes. Over the range of kelp densities that was of interest (6–24 stipes per habitat unit) and with an initial density of 30 fish per habitat unit, changes in the density of kelp had no discernable effect on per capita emigration rates of juvenile fish (linear regression, $P = 0.486$; Appendix C).

Experiment 2A investigated the effects of habitat complexity on mortality. In this experiment loss rates were affected by an interaction between fish number and habitat complexity ($P = 0.014$; also see Appendix A).

TABLE 3. Large-scale relationship between per capita mortality, habitat complexity (substrate relief), and density of juvenile blue rockfish (*Sebastes mystinus*) based on annual surveys among kelp beds.

Source	Coefficient	SE	P
Constant	3.05	0.835	0.00084
Initial density	0.097	0.03	0.00259
Substrate relief	−2.09	0.677	0.00392
Density × substrate relief	−0.035	0.021	0.11673

Notes: The best-fit multiple regression model was selected using Akaike's corrected Information Criterion. Model adjusted $r^2 = 0.575$. For the regression, ss = 79.172, $F_{3,35} = 18.125$, $P < 0.00001$. For the residual, ss = 50.961.

TABLE 4. Large-scale relationship between per capita mortality, habitat complexity (substrate relief), and density of juvenile kelp, gopher, and black-and-yellow (KGB) rockfish (*Sebastes* spp.) based on annual surveys among kelp beds.

Source	Coefficient	SE	P
Constant	2.74	0.304	<0.00001
Initial density	0.148	0.029	0.00001
Density × substrate relief	−0.07	0.018	0.00052

Notes: The best-fit multiple regression model was selected using Akaike's corrected Information Criterion. Model adjusted $r^2 = 0.529$. For the regression, ss = 92.3, $F_{2,36} = 21.61$, $P < 0.00001$. For the residual, ss = 76.89.

Because there was no effect of either prey density (Johnson 2006) or kelp density on per capita emigration of prey from these habitat units (experiment 2B), any density-dependent loss of fish was interpreted as an effect of mortality. Although mortality increased with initial number of fish (i.e., mortality was density dependent), the strength of density-dependent mortality was higher for the high complexity treatment. This change appeared to be due to differential effects of increased kelp cover as prey density increased. At low numbers, prey fish in high complexity treatments suffered less mortality. However, when prey number was high, prey mortality was high regardless of habitat complexity (Fig. 2).

Large-scale mortality patterns

For blue rockfish, yearly mortality was best described by a model containing initial density, substrate relief, and initial density × substrate relief as predictors (Table 3). These results indicated that mortality of blue rockfish increased with their initial density and decreased with increased substrate relief (negative coefficient of site effect) and that the strength of density-dependent mortality was reduced by increased substrate relief (negative coefficient of interaction). The best-fit model of mortality for KGB rockfish included initial density and initial density × substrate relief as predictors (Table 4). For KGB rockfish, mortality also increased with initial density, although in this case the primary effect of increased site relief was to reduce density-dependent mortality (negative coefficient of interaction; nonsignificant effect of site relief). Although recruitment was variable for both species, recruitment was significantly correlated with substrate relief for KGB rockfish ($r = 0.35$, $P = 0.029$), but not for blue rockfish ($r = 0.242$, $P = 0.21$).

DISCUSSION

Predator density and functional response

Predation is an important source of density-dependent mortality of many taxa (see references in Cappuccino and Price [1995], Hixon and Webster [2002], Hixon and Jones [2005]). Many studies have quantified functional responses of predators; however, relatively few studies have examined the effects of multiple predators on

individual predator response (reviewed by Sih et al. [1998]). Those that have typically find evidence for predator interference, although some cases indicate predator facilitation (Sih et al. 1998). Moreover, for several species that have been well-studied, separate experiments have indicated differences in the form of their functional response, potentially due to differences in prey type and preference (Hassell et al. 1977). This evidence suggests that predatory species may exhibit a range of different responses, depending on local conditions. The results of this study suggest that a form of predator facilitation occurred. In particular, as predator density increased, their functional response changed from one that approached saturation (Type II) to one that accelerated over the range of prey densities encountered (i.e., a Type III response). Although groups of juvenile bocaccio did not exhibit any complex and coordinated behavior, some simple advantages of group predation may explain the increase in prey consumption at high predator densities. Observations from the field and the laboratory suggest that predatory bocaccio rockfish would often cue in on conspecifics that were actively hunting and increase their own activity, thereby detecting previously unnoticed prey. Predators were also more inclined to attack erratically moving prey, and predators were more effective when attacking prey that were already being pursued. The observed acceleration of functional response when predators are in high densities may be due to several factors including (1) increased prey detection due to a shortage of refuge when prey are in high densities; (2) increased prey detection due to cues from other active predators; and (3) increased efficiency of group hunting.

Even though the fishes used in this experiment were small, their movement patterns were certainly restricted. Predation rates were likely to be unnaturally high within the enclosures. However, key biases to consider are those that would artificially change the form of the functional response as predator density increased. Within this experiment, one such source of bias may have been the inability of prey to redistribute themselves as predator density (and predation pressure) increased. However, I believe that the mechanisms that lead to an accelerating functional response as predator density increased (i.e., increased prey detection and increased efficiency of group hunting) affect natural predator–prey interactions in this system and are likely to influence the dynamics of prey populations. Both juvenile KGB rockfish and their predators tend to be distributed in aggregations. Even when kelp canopy habitat is extensive and uniform, the distribution of juvenile rockfish tends to be patchy, with juveniles aggregating around particularly dense clusters of kelp (Carr 1991, Nelson 2001). As density of the local population (e.g., fish within an entire kelp bed) increases, the distribution of juvenile rockfish remains patchy although the mean group size increases (Appendix D). Within this system encounters between small groups of predators and prey

occur frequently, and the cumulative effects of these predator–prey interactions may cause large changes in prey population size. Within the experimental enclosures, prey could not escape predators by swimming away; however, this situation may be the norm (Houk and McCleneghan 1992) since juvenile KGB rockfish are much slower swimmers than their predators (primarily juvenile boccaccio and other 1–2-yr-old rockfish). Moreover, over 100 person-hours spent conducting timed, behavioral observations of predators and prey within this system suggest that KGB rockfish do not redistribute themselves in response to predation risk. Instead, when exposed to predators, KGB rockfish tend school more tightly or to take refuge in the kelp (Johnson 2006). Similar results have often been found for the behavior of small prey fish under predation risk (Savino and Stein 1982, Magurran and Pitcher 1987, Sogard and Olla 1997, Lehtiniemi 2005).

Habitat complexity and strength of density dependence

Although predation rates are typically reduced in structurally complex habitats, experiment 2A demonstrated that increasing habitat complexity actually increased the strength of density-dependent mortality. This result may be due to the effects of habitat complexity on prey detection. Predators can generate density-dependent mortality via an aggregative response when they are attracted to and more likely to consume prey that are in larger groups (Hassell and May 1974). However, prey detection may be reduced in complex habitat (e.g., Savino and Stein 1982, Beukers and Jones 1997). One explanation for the experimental results described here could be that at low numbers of prey, additional kelp cover reduced the probability of prey being detected and/or captured. However, at high prey numbers, prey were more active and schools occupied a greater volume of water (*personal observation*). It may be that within my experimental array, predators could detect large prey schools, despite increased densities of kelp in some treatments. The effect of increased complexity would therefore be a strong reduction in mortality at low densities, but a weak reduction in mortality at high densities. Such an effect would lead to an increase in the strength of density-dependent mortality.

Large-scale mortality patterns

Rates of predation on juvenile rockfishes are high (Hallacher and Roberts 1985, Adams and Howard 1996, Hobson et al. 2001), and at the scale of an entire kelp bed, density-dependent mortality of juvenile rockfishes is likely to be generated by an accelerating (e.g., Type III) functional response of predators and/or a shortage of prey refuge (Johnson 2006). Structural complexity of habitat is often proportional to the available refuge space for prey (see Steele [1999] and Anderson [2001] for examples with kelp forest fishes). In the patterns of large-scale mortality reported here, increased topographic relief of substrata provided a substantial

reduction in the strength of density-dependent mortality. These results are concordant with a dynamic refuge model of density dependence (Lynch et al. 1998), where density-dependent mortality is generated by predation and a shortage of refuge space. Variation in the amount of prey refuge provided by habitat structure may have been responsible for among-population variation in the strength of density-dependent mortality (see Forrester and Steele [2004] for a similar example).

In this study, the effects of habitat complexity on the strength of density-dependent mortality differed between small-scale experiments and large-scale observations. However, the effects of habitat complexity on the strength of density dependence in prey mortality may depend on which type of predatory response generates density-dependent mortality (i.e., functional or aggregative) and how habitat complexity modifies predator response. In experiment 2A, density-dependent mortality was likely to be caused by predator aggregation. Habitat complexity increased the strength of density-dependent mortality, probably because complex habitat affected predator's ability to detect prey at low prey densities. At large scales, aggregation of predators to reefs with high densities of prey fish was unlikely, since the major predators of juvenile rockfish are other, resident reef fishes (Hallacher and Roberts 1985, Love et al. 1991, Hobson et al. 2001). Within nearshore reefs, density-dependent mortality of juvenile rockfishes may be caused by an accelerating functional response and/or a shortage of prey refuge. In such situations, increased complexity may decrease the strength of density-dependent mortality by providing more refuge (Murdoch and Oaten 1975, Lynch et al. 1998, Forrester and Steele 2004).

Consequences of variation in the strength of density dependence

This study suggests that both local predator density and habitat complexity can alter the strength of density-dependent mortality of juvenile fishes. Such variation in density dependence may have substantial consequences for both the detection of density dependence and the dynamics of fish populations. Variation in the strength of density dependence that is driven by features of the habitat (e.g., predator density and habitat complexity) may obfuscate any density-dependent patterns in vital rates and may lead to the spurious conclusion that density-dependent mortality is unimportant or not operating. This may be especially problematic if the strength of density dependence is negatively correlated with abundance ("cryptic density dependence" sensu Wilson and Osenberg [2002] and Shima and Osenberg [2003]). In this system recruitment was positively correlated with site relief. However, these patterns could also have resulted from greater post-settlement mortality occurring in low-relief habitats before the initial censuses. Correlations were significant for KGB rockfish, but not for blue rockfish. Although density-

dependent mortality was detected for both species, the data suggest that KGB rockfish exhibited a form of cryptic density dependence. Overall, strength of density-dependent mortality of KGB rockfish was likely to be underestimated. This pattern may be because of the tendency of fish to recruit in higher numbers to sites where the strength of density dependence was low (i.e., high-relief sites) and/or a greater tendency to underestimate recruitment at low-relief sites.

Variation in the strength of density-dependent mortality may also affect the relative importance of processes that influence the structure and dynamics of open populations (Chesson 1998, Schmitt et al. 1999). The strength of density-dependent mortality will determine the degree to which local population size is likely to fluctuate in response to variable recruitment. When and where density-dependent mortality is weak, populations may fluctuate widely, reflecting variable supply. Large recruitment fluctuations may result in local species assemblages that appear to be stochastic or "nonequilibrial" in their composition and may include those that are characterized by recruitment limitation (Doherty 1981) or competitive lotteries (Chesson and Warner 1981). Where and when density-dependent mortality is strong, local populations may fluctuate less and composition of species within the community may appear to be more deterministic and stable. Indeed, community stability and dynamics may depend heavily on how features of the local food web (e.g., predator density) and habitat (e.g., structural complexity) affect processes that regulate individual populations.

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APPENDIX A

A table showing analysis of covariance (ANCOVA) results of the effects of habitat complexity on proportional loss from isolated units of habitat (*Ecological Archives* E087-068-A1).

APPENDIX B

A table showing a summary of group sizes for juvenile rockfish encountered during underwater visual transects (*Ecological Archives* E087-068-A2).

APPENDIX C

A figure showing the relationship between kelp density and per capita emigration of kelp, gopher, and black-and-yellow (KGB) rockfish from experimental habitat units (*Ecological Archives* E087-068-A3).

APPENDIX D

A figure showing the relationship between mean group size of juvenile kelp, gopher, and black-and-yellow (KGB) rockfish encountered during underwater visual transects and the average density of fish within entire kelp beds (*Ecological Archives* E087-068-A4).