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The relative importance of predation and competition in two reef fishes

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Abstract Competition and predation may both strongly influence populations of reef fishes, but the importance of these processes relative to one another is poorly understood. I quantified the effects of predation and competition on the growth and survival of two temperate reef fishes, *Lythrypnus dalli* and *Coryphopterus nicholsii*, in field experiments in which I manipulated the densities of the two species and the abundance of predators (using enclosure cages) on small replicate patch reefs. I also evaluated the influence of predators on the behavior of the two species to help interpret the mechanisms of any predatory influences on growth or survival. Predation was much more important than competition (inter- or intraspecific) in *Lythrypnus*. For *Coryphopterus*, neither competition nor predation were particularly important. Behaviorally, both species responded to predators by reducing foraging rate and hiding. This altered behavior, however, had no repercussions for growth or survival of *Coryphopterus*. In contrast, *Lythrypnus* grew more slowly and suffered greater mortality when exposed to predators. Interspecific competition did not significantly influence either species. Intraspecific competition did not affect the growth of *Coryphopterus*, but survival tended to be lower at high densities. Growth of *Lythrypnus* was depressed by intraspecific competition, but survival was not, except that, in the presence of predators, survival was density dependent. In contrast to the historical emphasis placed on the role of competition, this study indicates that predation can be more important than competition in determining patterns of abundance of

some reef fishes. For example, predators not only influenced foraging of both *Lythrypnus* and *Coryphopterus*, but they also reduced growth and survival of *Lythrypnus*, and therefore appear to help maintain the marked habitat segregation between the two species.

Key words Predation · Intraspecific competition · Interspecific competition · Reef fishes · Relative importance

Introduction

Interspecific competition is an important determinant of population densities and the distribution of a variety of organisms (reviewed in Connell 1983; Schoener 1983). Yet for reef fishes, the importance of this process relative to others remains poorly understood. Historically, interspecific competition has been assumed to be a crucial process structuring reef-fish assemblages (e.g., Smith and Tyler 1972; Roughgarden 1974; Ehrlich 1975; Ebeling and Hixon 1991); however, experimental manipulations of potential competitors have yielded mixed results. Some studies have shown that interspecific competition has little or no effect on population densities (e.g., Doherty 1982, 1983; Jones 1987a, 1988; Roberts 1987), whereas others have documented strong effects (e.g., Hixon 1980; Larson 1980; Shulman et al. 1983; Sweatman 1985; Robertson and Gaines 1986; Jones 1987b; Schmitt and Holbrook 1990; Robertson 1996).

In contrast to the historical emphasis on competition, predation is now often believed to be a strong determinant of reef-fish abundance (reviewed in Hixon 1991). However, none of the experimental studies on competition (or predation) in reef fishes have allowed the importance of competition to be evaluated relative to the effects of predation, a process that Sih et al. (1985) found to be generally more important than competition in other taxa. Rather than “argue” about the relative importance of competition and predation, we need studies that quantify their relative importance (Sih et al. 1985).

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Likewise, the importance of *intraspecific* competition in reef fishes (a commonly detected process; reviewed in Jones 1991) has not been evaluated relative to predation. The importance of competition (inter- or *intraspecific*) in reef fishes may hinge upon predation, which can modify the outcome of competitive interactions, either by eliminating them (e.g., Paine 1966) or intensifying them (e.g., Werner et al. 1983). Even when there are no interactions between competition and predation, competition may be relatively unimportant if its effects are small relative to those of predation.

In this study, I evaluated the relative importance of interspecific competition, *intraspecific* competition, and predation in two temperate reef fishes. In a series of experiments, I manipulated the densities of bluebanded gobies (*Lythrypnus dalli*), blackeye gobies (*Coryphopterus nicholsii*), and predators. In southern California, where this study was conducted, these two common gobies frequently co-occur and exhibit a pattern of distribution consistent with interspecific competition. In areas of mixed rock and sand, *Coryphopterus* reaches its greatest densities (over 20/m²), but in these areas *Lythrypnus* is relatively rare, even though it occurs at high densities (>120/m²) in other rocky microhabitats (M. Steele, unpublished data). This pattern could be caused by the larger [up to 90 mm standard length (SL)] and more aggressive *Coryphopterus* behaviorally excluding the smaller (<50 mm SL) *Lythrypnus* from the rock/sand microhabitat. Furthermore, because both species are primarily planktivorous, they may compete for food, which alone could cause or intensify microhabitat partitioning. On the other hand, these patterns of distribution may be caused by other factors, such as differences in habitat preference or differential habitat-specific risks of predation.

At Santa Catalina Island (33°27'N, 118°29'W), where the experiments were conducted, the most common predator of the two gobies is the kelp bass, *Paralabrax clathratus*. It is the dominant piscivore in all microhabitats used by the gobies and comprises about 90% of all piscivorous fishes on reefs at Santa Catalina Island (M. Steele, unpublished data). In the field, kelp bass are commonly seen hunting gobies, and readily consume both goby species in laboratory aquaria (personal observations). In the rock/sand microhabitat, *Lythrypnus* may be especially vulnerable to predators because it is brilliantly colored and active, and thus easily detected against the light-colored sand background, whereas *Coryphopterus* is cryptic, matching its color to that of the sand, and much less active.

In this study, I tested whether interspecific competition could account for the low densities of *Lythrypnus* found in the rock/sand microhabitat favored by *Coryphopterus*. I did this by conducting experiments on small rock rubble reefs built on a sand bottom. During these experiments, I also tested for *intraspecific* competition in the two species and compared the relative effects of each type of competition. Further, I compared the relative importance of both types of competition with

that of predation, and I tested for interactions between competition and predation.

Materials and methods

Study site

To assess the relative importance of *intraspecific* competition, interspecific competition, and predation, I conducted three experiments on the north side of Santa Catalina Island in Big Fisherman Cove. For the experiments, I used small artificial reefs built in a sandy area that was bordered on one side by a large continuous rocky reef (for maps and diagrams of the site, see Steele 1997a). Predators in this sandy area are the same as those found in more rocky habitats, with the addition of the barred sand bass (*P. nebulifer*). The majority of predators in the area appeared to reside primarily on the nearby large rocky reef and ventured off the reef to forage.

Tests for effects of competition and predation

In the absence of predators, I explored the effects of competition (both *intra-* and *interspecific*) on *Lythrypnus* and *Coryphopterus* with two experiments (12 July–6 August 1992 and 15 August–8 September 1992). In a third experiment (19 July–12 August 1993), I examined predatory and competitive effects concurrently.

All experiments were conducted on a grid of standardized 1-m² rock rubble reefs. To minimize differences in habitat quality, each reef consisted of a standard number and size distribution of rocks (32 rocks 5–30 cm long, except that in the third experiment the number of rocks was doubled to ensure survival of at least some gobies on reefs exposed to predators). Reefs consisted of a monolayer of rocks with cracks, crevices, and small patches of sand between them. Reefs were spaced 10 m apart from each other to minimize exchange of gobies among reefs, and built in three rows parallel to the large continuous reef along the south side of the cove. The three rows of reefs were 10, 20, and 30 m from the edge of the continuous natural reef. Depth increased with distance from the natural reef: the average reef depth on the three rows was 7, 9, and 11 m, and all reefs within a row varied less than 3 m in depth.

Within each row of reefs, treatments (see sections below describing each experiment) were assigned randomly, with the additional condition that identical treatments in neighboring rows could not be adjacent. One replicate of each treatment was included in each row of reefs (i.e., $n = 3$), and was stocked with a size range of each goby species that reflected natural size distributions, except that very small juveniles (*Lythrypnus* <16 mm and *Coryphopterus* <20 mm) were not used because handling mortality was unacceptably high. *Lythrypnus* used in the experiments ranged from 16 to 36 mm, and *Coryphopterus* ranged from 20 to 85 mm. Since *Lythrypnus* matures at 16–20 mm (Behrents 1983; St. Mary 1993), most of the individuals stocked were adults. *Coryphopterus* settles at a size of 15–25 mm (M. Steele, unpublished data) and matures at about 45 mm (Wiley 1973), so the experiments used size distributions that included recently settled individuals as well as adults. However, most individuals used were juveniles, mimicking natural populations during summer. Initial lengths were marked on each fish with a subcutaneous injection of acrylic paint. In each experiment, fish present on the reefs after 24 days were collected by scuba divers using handnets and quinaldine, an anesthetic. Experimental fish were distinguished from recruits (fish that had settled from the plankton onto the reefs during the experiments) and immigrants by the presence of acrylic marks.

I focused on two responses to competition and predation: changes in survival and growth. Survival was potentially confounded with emigration, but by separating reefs from other suitable habitat by a minimum of 10 m of bare sand, I minimized the

effect of migration. Systematic searches for marked gobies on experimental reefs not stocked with gobies, and also on the only nearby natural reef, indicated that only a very small fraction ($\leq 1.1\%$) of the experimental fish successfully migrated to other reefs (Steele 1995, 1997b). Therefore, I estimated survival by dividing the number of marked fish remaining on each reef after 24 days by the number originally stocked. Growth (change in SL) of individuals over the course of the experiment was determined by remeasuring each fish after 24 days.

Experiments 1 and 2: competitive effects in the absence of predators

In these experiments I tested for effects of competition (intra- and interspecific) in the absence of predators. Both experiments employed essentially the same design. I used five treatments to explore competition: ambient density *Lythrypnus* (L), double ambient density *Lythrypnus* (2L), ambient density *Coryphopterus* (C), double ambient density *Coryphopterus* (2C), and ambient density *Lythrypnus* plus ambient density *Coryphopterus* (L + C). An additional treatment, zero density of both species, was used to evaluate emigration of tagged gobies from experimental reefs. "Ambient" density approximated the average density of conspecifics experienced by each species in qualitatively good habitat on nearby natural reefs.

I used different "ambient" densities in experiments 1 and 2. For *Lythrypnus*, I altered the density to reflect a seasonal increase in average density in natural populations (density increases throughout the summer due to seasonal settlement). In the first experiment, 20 individuals per reef were stocked for the ambient-density treatments, whereas in the second experiment I used 30 individuals. For *Coryphopterus*, I used 5 individuals per reef in the first experiment and 15 per reef in the second experiment for the ambient-density treatments. Although 5 fish/m² was approximately the average density in natural populations of *Coryphopterus* during both time periods (Steele 1997a), I increased densities of *Coryphopterus* because loss of this species from reefs in experiment 1 was high, which limited my ability to investigate responses of either species to competition. Additionally, in experiment 2, I restocked missing *Coryphopterus* (but not *Lythrypnus*) weekly to maintain differences between density treatments. To test for competitive effects on *Coryphopterus* in experiment 2, I analyzed growth and survival of only those *Coryphopterus* initially stocked on the reefs (not those from the various restockings).

In both experiments, each reef was enclosed in a 1 × 1 × 0.67 m high cage. Cages consisted of frames (made of 22-mm-diameter PVC pipe) covered on all sides by 19-mm-mesh plastic netting. Movement of gobies on or off the reefs was not restricted by this mesh size, but all predators larger than about 80 mm SL were excluded. Cages were scrubbed clean of fouling organisms approximately twice weekly. Throughout the experiments, divers counted visible gobies on every reef at least twice weekly; each reef was observed for 5 min during these counts.

Experiment 3: predatory and competitive effects

To compare the effects of predation with those of competition, I conducted an experiment that was similar in design to the previous two experiments, except that predation was also included as a factor. As in the previous experiments, I stocked various combinations of densities of the two gobies on the reefs. Half of the reefs were exposed to predators and the other half were not; predators were excluded with the same cages used in experiments 1 and 2. Predator-exposed reefs were not uncaged, instead, they were enclosed in cages that lacked netting on the lower half of one side (i.e., a 0.33 × 1 m opening). These partial cages were used because *Lythrypnus* (but not *Coryphopterus*) is affected by cage artifacts (Steele 1996), but the partial cages do not differ in their effects on *Lythrypnus* from complete enclosure cages (Steele 1996). Hence, by comparing survival, growth, and behavior of fish in the partial cages with those of fish in complete cages, any differences between

the two treatments could reliably be attributed to effects of predators (and not cage artifacts). Fish stocked in partial cages were given several hours to acclimate to their new homes before they were exposed to predators. I accomplished this by initially covering the open half-side of the partial cages with a piece of netting. After the netting was removed from the open half-side of the partial cages, predators were frequently observed inside this predator-exposed treatment.

I used four goby-density treatments to evaluate competition: L, 2L, L + C, and C (plus a zero-density treatment to evaluate emigration). Given logistical constraints, I eliminated the 2C treatment, which precluded the evaluation of intraspecific competition in *Coryphopterus*. Ambient densities were the same as in experiment 2 (ambient *Lythrypnus* = 30, and ambient *Coryphopterus* = 15) and neither species was restocked during the experiment. The four goby-density treatments were crossed with two levels of predator exposure (exposed or unexposed) for a total of 8 treatment combinations. Each combination was included once in each of the three rows of reefs (i.e., $n = 3$), resulting in 24 experimental reefs stocked with gobies. All visible gobies on each reef were counted at least twice weekly and the maximum number of piscivorous fishes (kelp bass and barred sand bass) present on or within 1 m of each reef (including completely caged reefs) during the standard 5-min goby-counting period was also recorded.

To evaluate possible mechanisms underlying the influences of predators on growth and survival, I assessed behavioral responses of gobies to predators using time budgets (recorded to the nearest second). Haphazardly selected focal individuals were observed for 10-min periods between 1100 and 1630 hours. On different days, four 10-min observations were made on each reef for *Coryphopterus*, and five 10-min observations were made per reef for *Lythrypnus*. The number of bites of food taken, moves made, and the total time spent foraging, perching on top of rocks, clinging to sides of rocks, hiding underneath rocks, resting next to rocks on sand (within 5 cm of rocks – inside or outside of cages), and resting on sand away from rocks (>5 cm – inside or outside of cages) were recorded. (*Coryphopterus* would venture outside cages and rest upon the sand, but *Lythrypnus* never ventured outside cages). The presence of predators on reefs (inside partial or complete cages) during focal observations was also noted.

Analysis

Survivorship and growth

I used analysis of covariance (ANCOVA) and a priori comparisons to test for effects of competition and predation. In the statistical models, I included competition treatment (three treatments for each species: L, L + C, and 2L for *Lythrypnus*, and C, L + C, and 2C for *Coryphopterus*), and predator exposure (closure or partial cage, experiment 3 only) as fixed, categorical factors. To reduce unexplained variation and thereby allow for more powerful tests, I initially included "row" (a categorical factor; reefs were built in 3 rows) and "position" (position within a row, a covariate representing a potential gradient in conditions from the mouth to the back of the cove in which the experiments were conducted) in the models. I considered "row" to be a fixed effect, instead of a random effect, because rows spanned a gradient of depth and distance from the nearby large reef and included all possible rows. To allow for more powerful tests of the influences of competition and predation, "row" and "position" were eliminated from models and pooled in the error terms when nonsignificant ($P > 0.25$ for the categorical factor "row" and $P > 0.05$ for the covariate "position"; Winer et al. 1991). Effects of intra- and interspecific competition were tested with a priori comparisons in the two experiments in which predators were not manipulated (experiments 1 and 2). Intraspecific competition was tested by comparing the ambient-density treatment vs. the twice-ambient-density treatment (i.e., L vs. 2L for *Lythrypnus*, and C vs. 2C for *Coryphopterus*). Interspecific competition was tested by comparing the ambient-density treatment vs.

the ambient-density + ambient-density-heterospecifics treatment (i.e., L vs. L+C for *Lythrypnus*, and C vs. L + C for *Coryphopterus*).

Because replication was low ($n = 1$ reef/treatment per row) and the number of independent variables in the ANCOVAs was high, it was impractical to test all possible interactions among “main effects.” For experiments 1 and 2, I did not test for differences in competitive effects among rows of reefs (i.e., interactions between row and competition treatment) since such differences were not expected on the basis of reef location, nor were they a focus of the study. For experiment 3, I tested for interactions between “row” and “predator exposure” because predator densities differed among rows (see Results). To investigate whether predators influenced competition, I tested for an interaction between “predator exposure” and “competition treatment.” No other interactions were initially included in the ANCOVA models. When the covariate “position” explained a significant proportion of the variation, interactions between this variable and the categorical variables were tested to assess the assumption of homogeneity of slopes. Because of limited replication, it was sometimes necessary to test interactions between the covariate and categorical variables sequentially, rather than simultaneously including all possible interactions in the statistical models. In every case, these interactions were not significant ($P > 0.05$) and they were subsequently eliminated from the model. Where necessary, data were transformed to meet assumptions of normality and homoscedasticity (see Results and pertinent tables for details of transformations used).

Growth of both goby species is influenced by body size (measured as SL). To make the most accurate tests for influences of competitors and predators on growth, I removed statistically the influence of body size on growth before testing for effects of competitors and predators. I did this by first running a simple linear regression of individual growth on initial length using all fish for each species in each experiment. I then calculated for each reef the mean of the residuals from the regression of growth on length. The influences of competitors and predators (as well as position and row) on growth were then tested with ANCOVA as described in the preceding paragraphs, using the mean residuals as the response variable.

Quantifying the relative importance of competition and predation

I quantified the contributions of competition (intra- and interspecific) and predation by calculating the “intensity” (or magnitude) of each process (Welden and Slauson 1986; Steele 1997a) as the difference between two treatments (e.g., with and without interspecific competitors) expressed as a percent of the grand mean in each experiment. I scaled intensity to the grand mean to make it readily comparable among processes. For experiment 3, however, I scaled intensity to the mean of caged reefs only, which made the measure more comparable among the three experiments. For example, the intensity of intraspecific competition in experiments 1 or 2 was calculated as mean survivorship in the double-ambient-conspecific-density treatment minus mean survivorship in the ambient-conspecific-density treatment, divided by the grand mean (in experiment 3, it was divided by the mean on caged reefs), multiplied by 100. When the covariate “position” explained significant variation in a response variable, I calculated the intensity of other factors (e.g., intraspecific competition in *Lythrypnus*) using adjusted least-squares means (i.e., for treatments L and 2L) from final ANCOVA models to remove the influence of the covariate.

Mechanisms: behavioral responses to predators

In experiment 3, I gathered data on behavioral responses of the two gobies to predators. With these data, I used two approaches to explore the influences of predators. I used ANCOVA (as described in the preceding section) to test for differences in behavior of fish on

predator-exposed reefs (partially caged reefs) versus behavior on reefs in predator-exclosure cages. This approach assessed differences in behavior between the two reef types, but, for two reasons, did not accurately assess the effects of predators on prey behavior. First, because small predators were sometimes present in “exclosure” cages, this treatment was not truly predator free. Second, predators were not always present on predator-exposed reefs, so measurements of behavior made during times when predators were absent did not reflect the direct behavioral responses of prey to predators. To more accurately assess the direct influence of predators on goby behavior, I divided the behavioral observations on each reef into two groups: observations made when predators were absent, and observations made when predators were present (only when predators were inside partial cages or “exclosures”), regardless of the predation treatment. This categorization provides a somewhat conservative test of the response of gobies to predators because I based the distinction between predators present versus absent on the presence of predators inside cages. However, predators outside the cages could be within centimeters of the focal goby, which induces predator avoidance behavior (personal observations). For each reef, I pooled all observations within each condition (predators present or absent). For each condition, I calculated foraging rate, and the proportion of time spent moving, perching on top of rocks, clinging to sides of rocks, hiding underneath rocks, resting next to rocks on sand (within 5 cm of rocks), and resting on sand away from rocks (> 5 cm). I then evaluated the effects of predators on goby behavior by testing for differences between the two groups of observations using independent t -tests (or Mann-Whitney U -tests when the data were extremely non-normal). I excluded rates and proportions that were based on < 60 s of observation (invariably predators present) because they were poor estimates of infrequent behaviors.

Results

Competition

In the absence of predators (i.e., on reefs in exclosure cages), *Lythrypnus* experienced intraspecific competition. Growth was significantly slower at high densities in experiments 1 and 2 (Table 1, Fig. 1c) and tended to be slower at high densities in experiment 3 (Fig. 1c), but survival was not affected by density (Tables 1 and 2, Fig. 1a). In the presence of predators (experiment 3, partial cages), however, survival was lower on high-density reefs (a priori test for difference between L and 2L treatments on predator-exposed reefs only: $F_{1,3} = 18.7$, $P = 0.02$; Fig. 1a).

Coryphopterus exhibited lower survival at high densities (25–42% lower in the 2C treatment than in the C treatment; Fig. 1b), but this difference only approached statistical significance in experiment 2 ($P = 0.051$, Table 1). Growth of *Coryphopterus* was not significantly influenced by intraspecific competition (Table 1, Fig. 1d).

I did not detect any significant effects of interspecific competition. Growth and survival of both species was not significantly reduced by heterospecific gobies (Tables 1, 2, Fig. 2), although survival of *Coryphopterus* always tended to be lower on reefs shared with *Lythrypnus* than on reefs without *Lythrypnus* (Fig. 2b). No similar trend towards reduced survival in the presence of *Coryphopterus* was evident in *Lythrypnus* (Fig. 2a).

Table 1 Results of a priori comparisons testing for effects of intra- and interspecific competition on survival and growth of *Lythrypnus* and *Coryphopterus*, in the absence of predators (experiments 1 and 2). For *Lythrypnus*, tests for intraspecific competition compared treatment L vs. 2L; tests for interspecific competition compared

treatment L vs. L+C. For *Coryphopterus*, tests for intraspecific competition compared treatment C vs. 2C; tests for interspecific competition compared treatment C vs. L + C. Survival of *Coryphopterus* was angularly transformed in experiment 2

Factor	Experiment 1			Experiment 2		
	F	df	P	F	df	P
<i>Lythrypnus</i>						
Survival						
Intraspecific competition	0.4	1,6	0.6	0.5	1,5	0.5
Interspecific competition	0.1	1,6	0.8	0.0	1,5	1.0
Growth						
Intraspecific competition	8.8	1,4	0.041	20.8	1,3	0.020
Interspecific competition	0.7	1,4	0.5	2.0	1,3	0.25
<i>Coryphopterus</i>						
Survival						
Intraspecific competition	0.4	1,4	0.5	5.9	1,6	0.051
Interspecific competition	0.8	1,4	0.4	1.3	1,6	0.3
Growth						
Intraspecific competition	1.4	1,4	0.3	0.7	1,6	0.4
Interspecific competition	0.1	1,4	0.8	3.0	1,6	0.13

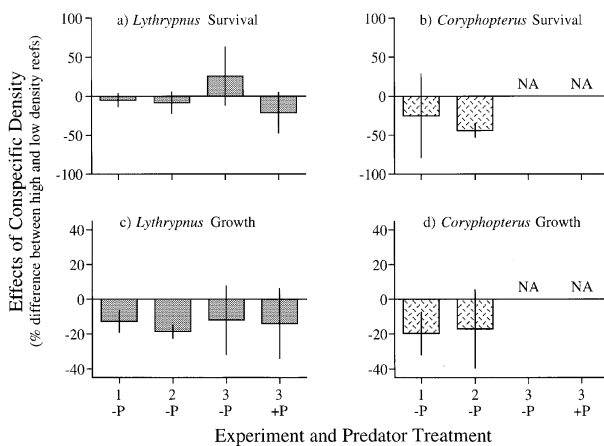


Fig. 1a–d Effects of conspecific density on survival and growth. Values are differences between reefs with high (2L or 2C) and low densities (L or C) of conspecifics expressed as a percent of the mean on low density reefs (± 1 SE). Adjusted least-squares means from final ANCOVA models were used if the covariate “position” explained significant variation in growth or survival. $-P$ and $+P$ indicate whether reefs were exposed ($+P$) to predators or not ($-P$). Note different y-axis scales in **a** and **b** vs. **c** and **d**. See Tables 1 and 2 for statistical tests of intraspecific competition. Mean survival (± 1 SE) of *Lythrypnus* = 0.70 ± 0.02 , 0.54 ± 0.03 , 0.34 ± 0.05 , and 0.16 ± 0.03 in experiments 1, 2, 3 $-P$, and 3 $+P$, respectively. Mean survival (± 1 SE) of *Coryphopterus* = 0.32 ± 0.09 , 0.42 ± 0.05 , 0.17 ± 0.04 , and 0.14 ± 0.05 in experiments 1, 2, 3 $-P$, and 3 $+P$, respectively. Mean growth (mm SL ± 1 SE) of *Lythrypnus* = 4.5 ± 0.2 , 3.4 ± 0.3 , 5.2 ± 0.4 , and 2.9 ± 0.4 in experiments 1, 2, 3 $-P$, and 3 $+P$, respectively. Mean growth of *Coryphopterus* = 6.5 ± 0.6 , 3.1 ± 0.3 , 6.1 ± 1.4 , and 6.8 ± 0.4 in experiments 1, 2, 3 $-P$, and 3 $+P$, respectively

Predation

Predators had strong effects on growth and survival of *Lythrypnus*, but not *Coryphopterus*. The average effect of predators was to reduce growth of *Lythrypnus* by 41%

and survival by 52%. The impact of predators on growth of *Lythrypnus* did not vary among the three rows of reefs [i.e., the “predation \times row” interaction was not significant ($P = 0.48$) and so was pooled in the error term of the model] (Fig. 3b). The effect of predators on survival, however, did vary among rows (Table 2, Fig. 3a). On reefs 20 and 30 m from the large continuous reef, survival was reduced drastically on predator-exposed reefs (Fig. 3a). However, there was no apparent effect of predators in the 10-m row, which may have been the result of small (< 80 mm SL) piscivorous kelp bass invading many of the predator “exclosure” cages in this row of reefs. Small bass were seen in 6 of 15 cages: in 3 of the 5 “exclosure” cages in both the 10- and 20-m rows, but in none of the cages in the 30-m row. (Small bass were never observed inside the cages used on all reefs during experiments 1 and 2.) Within bass-invaded cages, more bass were present in the 10-m row than the 20-m row: as many as 4 bass were seen within one cage in the 10-m row, while never was more than 1 bass seen in cages in the 20-m row. It is possible then, that survival of *Lythrypnus* in cage “exclosures” in the 10-m row was reduced by small predators to about the same level as in predator-exposed treatments (i.e., partial cages). Indeed, survivorship of *Lythrypnus* was 33% lower in cages known to have been invaded by bass than in cages in which bass were never seen, although this difference was only marginally significant (two-way ANOVA on survival on reefs only in “exclosure” cages, including the factors “bass invaded” – yes or no – and “row”: $F_{1,5} = 4.6$, $P = 0.08$). Growth of *Lythrypnus* in “exclosure” cages that were known to have been invaded by small bass was 25% lower than growth in bass-free cages, a significant difference (two-way ANOVA as described above: $F_{1,5} = 15.8$, $P = 0.01$). In summary, predators had strong effects on growth and survival of

Table 2 Results of AN(C)OVA testing for effects of predation and competition on survival and growth of *Lythrypnus* and *Coryphopterus* during experiment 3. Survival of *Lythrypnus* was angularly transformed. The term *Competition* tests for differences among three density/species treatments: L, L + C, and 2L. – in-

dicates that the term was not significant and so was pooled in the error term to allow more powerful tests of competition and predation. *Interspecific competition* tests for differences between treatments C vs. L + C. Intraspecific competition in *Coryphopterus* was not tested in experiment 3

Factor	Survival			Growth		
	F	df	P	F	df	P
<i>Lythrypnus</i>						
Predation	26.2	1,8	0.001	27.9	1,10	0.001
Competition	0.3	2,8	0.8	1.1	2,10	0.36
Predation × Competition	1.3	2,8	0.31	1.7	2,10	0.23
Row	0.8	2,8	0.5	4.0	2,10	0.053
Predation × Row	13.8	2,8	0.003	–	–	–
Position	–	–	–	–	–	–
<i>Coryphopterus</i>						
Predation	0.1	1,8	0.7	0.1	1,6	0.8
Interspecific competition	1.1	1,8	0.3	0.0	1,6	0.9
Predation × Interspecific competition	0.5	1,8	0.5	0.1	1,6	0.8
Row	–	–	–	–	–	–
Predation × Row	–	–	–	–	–	–
Position	–	–	–	–	–	–

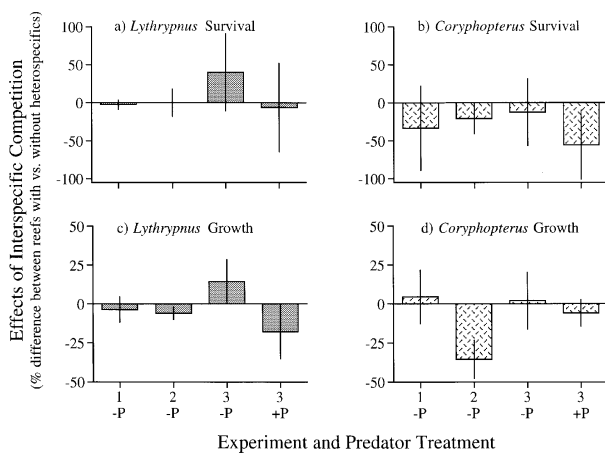


Fig. 2 Effects of interspecific competition on survival and growth. Values are differences between reefs stocked with heterospecifics (L + C) and reefs not stocked with heterospecifics (L or C), expressed as a percent of the mean on reefs without heterospecifics (± 1 SE). Adjusted least-squares means from final ANCOVA models were used if the covariate “position” explained significant variation in growth or survival. –P and +P indicate whether reefs were exposed (+P) to predators or not (–P). Note different y-axis scales in a and b vs. c and d. See Tables 1 and 2 for statistical tests of interspecific competition

Lythrypnus, even though effects on survival were variable spatially, probably at least partially due to differential invasion of cages by small predators.

On predator-exposed reefs (those in partial cages), among-row patterns of survival in *Lythrypnus* were not related to patterns in predator abundance: significantly fewer piscivorous predators (kelp bass and barred sand bass) were present in the 20- and 30-m rows than in the 10-m row (ANOVA $F_{2,33} = 9.10$, $P < 0.001$; mean maximum number of predators/reef counted within 1 m of reefs at any instant during standard 5-min counts of gobies = 2.56 ± 0.44 for the 10-m, 0.93 ± 0.24 for the

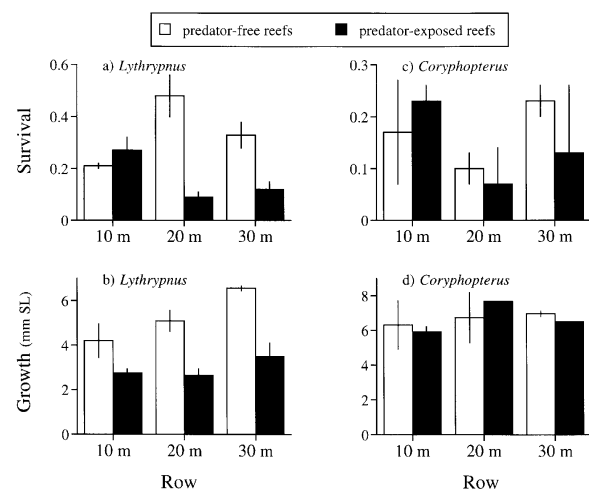


Fig. 3 Influences of predators on survival (proportion surviving) and growth of gobies in different rows of reefs. Replicate reefs were constructed at three distances from a large continuous rocky reef (10, 20, and 30 m) and half were exposed to predators (partial cages) and the other half were free of predators (exclusion cages). Values are means ± 1 SE. Note different y-axis scales. See Table 2 for statistical tests of interactions between row and predation

20-m, and 0.88 ± 0.21 for the 30-m row, $n = 12$). The lower predator density in the 20- and 30-m rows did not translate to increased survival in these rows. In fact, on predator-exposed reefs, survival of both gobies was highest in the row with highest predator density (the 10-m row, Fig. 3a, c).

Growth and survival of *Coryphopterus* were not affected by predators (Table 2, Fig. 3c, d). Furthermore, survival and growth of *Coryphopterus* did not differ between bass-invaded cages and non-invaded cages: survivorship was identical (17%) in invaded and non-invaded cages, and growth was very similar between the

two cage types: 6.14 ± 0.83 and 6.10 ± 1.19 for non-invaded and invaded cages, respectively.

Interactions between predation and competition

Using formal statistical tests for interactions (i.e., evaluating the interaction terms in the ANOVAs for experiment 3), I found no evidence for interactions between predation and competition (intra- or interspecific) (Table 2). There was, however, some qualitative evidence for an interaction between predation and intraspecific competition in *Lythrypnus*. In the absence of predators, survival was not affected by intraspecific competition (i.e., no difference between L vs. 2L treatments; Fig. 1a, Table 1), but when predators were present, survival was reduced at high densities (Fig. 1a; ANCOVA on predator-exposed reefs only, a priori test for difference between L and 2L treatments: $F_{1,3} = 18.7, P = 0.02$). Therefore, survival of *Lythrypnus* appeared to be density independent in the absence of predators and density dependent when predators were present.

Mechanisms: behavioral responses to predators

Predators influenced behavior of both goby species. ANCOVA, testing for differences between reefs in partial cages vs. reefs in predator “exclosure” cages, revealed significant differences in foraging rate, movement rate, and proportion of time spent under rocks by *Lythrypnus*, and in rate of movement and proportion of time spent perched on top of rocks by *Coryphopterus* ($P < 0.05$ in all cases). The precise effects of predators on behavior of gobies were clearer when observations were divided into two groups: those made in the absence of predators, and those made in the presence of predators, regardless of caging treatment. Behavioral responses of

the two gobies to predators were strong and very similar (Figs. 4, 5). In the presence of predators, foraging rate was reduced (to 14% and 10% of that in the absence of predators for *Lythrypnus* and *Coryphopterus*, respectively; Fig. 4), the proportion of time spent moving and perched on top of rocks was reduced (Fig. 5), and the proportion of time spent hiding under rocks increased (Fig. 5). All of these behavioral changes were statistically

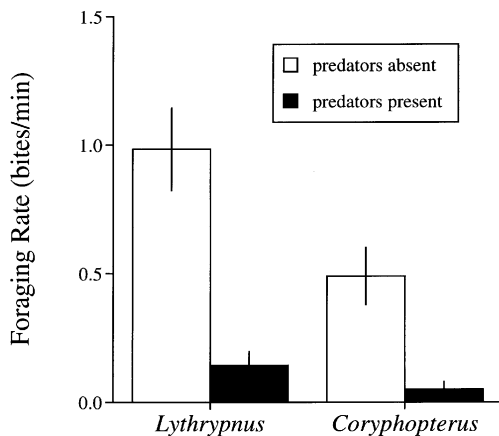


Fig. 4 Effects of predators on foraging rate. Error bars represent ± 1 SE, $n = 18, 13, 12,$ and 6 for the four bars, from left to right. In both species, foraging rates differed significantly ($P < 0.005$) between times when predators were present vs. absent

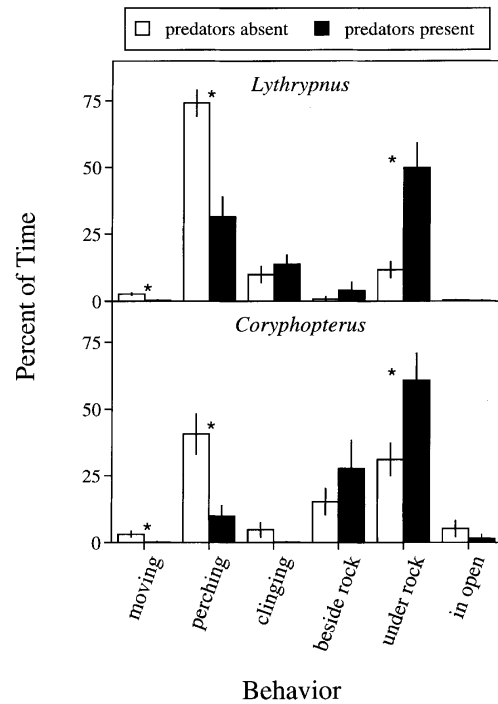


Fig. 5 Influences of predators on percent of time spent moving and resting in various positions relative to rocks. Error bars represent ± 1 SE. Asterisks indicate significant differences ($P < 0.05$)

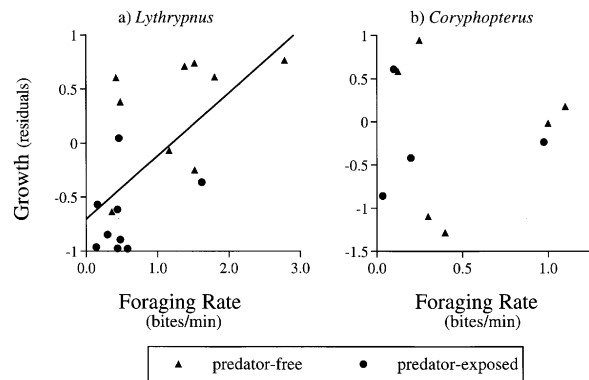


Fig. 6 Relationships between growth and foraging rate of the two gobies. Predator-free (caged) and predator-exposed (partially caged) reefs are distinguished. There was highly significant linear relationship between these variables for *Lythrypnus* [$P = 0.004$; foraging rate transformed to $\ln(100 \cdot x)$], but not for *Coryphopterus* ($P = 0.94$). Foraging rate is expressed as the mean/reef of standardized residuals from regressions of individual growth on initial size (mm SL) (see Materials and methods and Results for details). $n = 18$ and 10 for *Lythrypnus* and *Coryphopterus*, respectively

significant ($P < 0.05$, based on independent t -tests, or Mann-Whitney U -tests, with 26 and 16 df for *Lythrypnus* and *Coryphopterus*, respectively).

Reduced foraging in the presence of predators appeared to cause reduced growth in *Lythrypnus* since there was a positive relationship between growth and foraging rate (bites/min) in this species [simple linear regression on mean growth residuals (removing the relationship between growth and initial length, as for ANCOVAs, see Materials and methods); foraging rate transformed to $\ln(100*x)$: $r^2 = 0.41$, $P = 0.004$, $n = 18$, Fig. 6a]. However, there was no such relationship between growth and foraging rate in *Coryphopterus* (simple linear regression as for *Lythrypnus* except foraging rate was not transformed: $r^2 = 0.001$, $P = 0.94$, $n = 10$, Fig. 6b).

Discussion

Despite extensive research on interspecific competition, there remains considerable controversy about its importance. For example, as in this study, a number of investigations have failed to detect interspecific competition in reef fishes (e.g., Doherty 1982, 1983; Jones 1987a, 1988; Roberts 1987). On the other hand, many other studies have found strong effects of interspecific competition (e.g., Hixon 1980; Larson 1980; Shulman et al. 1983; Sweatman 1985; Robertson and Gaines 1986; Jones 1987b; Schmitt and Holbrook 1990; Robertson 1996). These variable results highlight a need to understand why competition exists between some species of reef fishes and not others. Notably, in every case where interspecific competition has been found, interference competition seems to be involved and strong agonistic interactions occur between the competing fishes. Relative to intraspecific aggression, interspecific agonism between *Lythrypnus* and *Coryphopterus* is rare (Steele 1995), which may in part explain the lack of competition between the two species during this study.

In contrast, intraspecific agonism in *Lythrypnus* and *Coryphopterus* is common (Steele 1995), and in the present study, intraspecific competition affected both goby species, either by decreasing growth (*Lythrypnus*) or survival (*Coryphopterus*). As in *C. nicholsii*, a recent study on a closely related reef fish, *Coryphopterus glaucofraenum*, also detected density-dependent survival while failing to detect density-dependent growth (Forrester 1995). It is likely that both Forrester's and the present study failed to detect density-dependent growth in the two *Coryphopterus* species because large differences in density among populations were not maintained due to density-dependent survival. While intraspecific competition caused density-dependent survival of *C. nicholsii* when predators were absent during the present study, density-dependent survival is not always indicative of intraspecific competition and, instead, such density dependence may be caused by predators (Murdoch and Oaten 1975).

Predators are widely believed to have important effects on reef-fish abundance (e.g., Shulman 1984, 1985; Sweatman 1984; Doherty and Sale 1985; Hixon and Beets 1989, 1993; Hixon 1991; Caley 1993; Carr and Hixon 1995; Steele 1996, 1997a; Beets 1997; Hixon and Carr 1997); however, relatively few studies have unequivocally demonstrated reductions of density by predators (but see Carr and Hixon 1995; Steele 1996, 1997a; Beets 1997; Hixon and Carr 1997). In this study, the effects of predators were not confounded with other factors (Steele 1996), so I can reliably attribute differences between reefs with enclosure cages (– predators) and reefs with partial cages (+ predators) to the effects of predators.

I found that predators greatly reduced survival and growth, and altered behavior of *L. dalli*. Given the positive relationship between growth and foraging in *Lythrypnus* (Fig. 6a), it seems likely that reduced growth in the presence of predators was ultimately caused by reduced foraging rates on predator-exposed reefs (Fig. 4). Predators did not influence survival or growth of *Coryphopterus*, yet behavior of this species was also strongly modified in response to predators. However, I probably underestimated the impact of predators on survival of both goby species because the + predators treatment (partial cages) severely limited the number of angles of approach predators could take to access prey. Moreover, some of the “predator-free” reefs were actually exposed to small predators that were able to squeeze through the mesh and invade the “enclosure” cages, further reducing the difference between predation treatments. Therefore, under more natural conditions, predators may affect survival of *Coryphopterus*, and indeed, other experimental studies have demonstrated just that (Steele 1996, unpublished data; G. Forrester and M. Steele, unpublished data). Nonetheless, in this study, the strong behavioral responses by *Coryphopterus* to predators did not result in reduced growth. Even though *Coryphopterus* reduced its foraging rate by about 90% when predators were present, this had no repercussions for growth. This lack of a predator-induced reduction in growth rate may indicate that growth of *Coryphopterus* is driven more by variation in energy expenditure (e.g., energy spent on territorial aggression) than by variation in energy input.

The impact of predators on *Lythrypnus* varied spatially (i.e., among rows of reefs): when large predators were absent (i.e., in enclosure cages – experiments 1, 2, and the caged reefs in experiment 3), survival was roughly even among rows of reefs (experiments 1 and 2: Steele 1995) or was lowest in the row of reefs 10 m offshore and higher in the 20- and 30-m rows (Fig. 3a). On reefs exposed to predators (those in partial cages in experiment 3), this pattern was altered: survival was *highest* in the 10-m row of reefs (Fig. 3a). Hence, prey were not eaten in proportion to their abundance (which would have resulted in equal rates of survival among rows). Predators also affected recruitment (accumulation of larval settlers over 3.5 weeks) of both gobies during experiment 3 in the same way: effects of

predators were smallest in the 10-m row of reefs (Steele 1997a). Taken together, these results indicate that a primary role of predators may be to alter spatial patterns of density established by settlement or other processes. Notably, predator density during experiment 3 was highest in the 10-m row, where survivorship on predator-exposed reefs was highest (Fig. 3), not lowest, as would be expected from the abundance of predators. This result suggests that knowledge of patterns of predator density may not be particularly useful for predicting spatial variation in predator impacts on prey populations, at least at some spatial scales (see also Connell 1996).

The relative importance of competition and predation

Considerable effort has been expended attempting to quantify the relative importance of various processes that affect populations, and a variety of approaches have been used (e.g., Welden and Slauson 1986; Menge 1991; Underwood and Petraitis 1994; Osenberg and Mittelbach 1996; Tyler 1996; Steele 1997a). I use a simple measure of the magnitude of the effect of a process, intensity, to assess the relative importance of competition and predation.

In this study, the relative importance of predation and competition varied greatly between the two fishes I studied. *Lythrypnus* was affected much more strongly by predation than by intra- or interspecific competition (Table 3). This result was observed regardless of whether the response of interest was survival or growth, although the relative influence of predation on survival was greater than its relative influence on growth (Table 3). In contrast, predation was the least important process affecting growth and survival of *Coryphopterus* (Table 3). The process having the greatest impact on *Coryphopterus* was intraspecific competition, although statistically this process did not have highly significant effects (Table 1).

It is not surprising that the importance of predation relative to competition was greater in *Lythrypnus* than *Coryphopterus*, particularly in the rock/sand microhabitat present on the reefs in this study. *Lythrypnus* is more colorful and more active than the cryptic *Coryphopterus* and so probably attracts more attention from predators, and since it is smaller it can be eaten by a wider size

range of predators. Hence, the observation that the density of *Lythrypnus* is low in the rock/sand microhabitat where the density of *Coryphopterus* is highest may be better explained by differential risk of predation than by interspecific competition.

Interactions among processes

In this study, there was a suggestion that predators may have induced density-dependent survival in *Lythrypnus* (indicating that they possibly induced competition). In the absence of predators, there was no evidence of density-dependent survival in *Lythrypnus* (Fig. 1a, Table 1), yet in the presence of predators, survival was density dependent (Fig. 1a). However, this interaction between competition and predation was not statistically significant (Table 2), possibly due to low statistical power and invasion of predator enclosures by small predators. Other studies (Steele 1997b; G. Forrester and M. Steele, unpublished data) have clearly demonstrated density-dependent survival of *Lythrypnus* where exposed to predators, but density-independent survival where predators are absent. This predator-induced density dependence could be caused by competition for limited refuge space, a type III functional response by predators, or by aggregation of predators to reefs with high densities of *Lythrypnus*. Determining which mechanism is the cause of density-dependent survival will be the subject of future work, but it is worth noting that I have never observed individual gobies being kept out of, or evicted from, already occupied refuges when predators were near, suggesting that active competition for limited refuge space is probably not the causal mechanism. Additionally, in the present study, I found no evidence of predator aggregation at high-density reefs (predator density at treatments L vs. 2L: 1.4 ± 0.5 vs. 1.4 ± 0.6 $n = 6$). At present, a type III functional response by predators seems the most likely cause of density-dependent survival in *Lythrypnus* exposed to predators.

Predators did not seem to alter the influence of intraspecific competition on growth of *Lythrypnus* (Fig. 1c). Because there was no food within the refuges used by the gobies, predators would not be expected to intensify competition for food, unless time spent sheltering limits foraging time. However, predators also re-

Table 3 Relative influences of predation, intraspecific competition, and interspecific competition on survival and growth of *Lythrypnus* and *Coryphopterus*, measured as the intensity (see Materials and methods) of the effects of each process. Values for predation are from experiment 3, while those for intra- and in-

terspecific competition are means (\pm SE) of experiments 1, 2, and 3. For *Coryphopterus*, values for intraspecific competition are means (\pm 1SE) from only experiments 1 and 2, since intraspecific competition in this species was not tested in experiment 3

Process	<i>Lythrypnus</i>		<i>Coryphopterus</i>	
	Survival	Growth	Survival	Growth
Predation	-52	-41	-14	-3
Intraspecific competition	-3 ± 4	-16 ± 2	-43 ± 12	-21 ± 1
Interspecific competition	4 ± 5	-3 ± 2	-34 ± 4	-13 ± 15

duced the density of *Lythrypnus*, which should have reduced any competitive effects on growth in this species. The net result of altered behavior and reduced density was no significant change in the effects of intraspecific competition on growth of *Lythrypnus*.

If risk of predation decreases with body size, reduced growth can reduce survival (e.g., Werner et al. 1983). However, in this system, I found no evidence for such an interaction: predator-induced mortality of *Lythrypnus* during experiment 3 was not size dependent (Steele 1995). Hence, in this system, processes that influence growth, e.g., in the present study, intraspecific competition and exposure to predators, may have no repercussions for survival, at least over the range of sizes used in this study. Growth and survival may often be unrelated if vulnerable size classes of organisms utilize habitats that reduce their risk of predation, thus eliminating their size-related predation risk (e.g., Stein 1977).

In conclusion, this study indicates that predation can be much more important than competition in setting patterns of abundance and in determining growth rate in some reef fishes, but also that the relative importance of competition and predation will vary widely among species. The task then is to develop a framework that allows us to predict in which situations predation will be more important than competition, and in which situations the reverse will be true.

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