Effects of shelter and predators on reef fishes

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Abstract

The abundance of reef fishes is often influenced by the availability of potential shelter sites. The most prevalent hypothesis explaining this relationship between fish density and shelter is that post-settlement predation causes greater mortality in areas with little shelter vs. areas with abundant shelter. This hypothesis was tested with a set of field experiments, in which the availability of shelter and exposure to predators were manipulated orthogonally. The effects of shelter and predators were measured for recruitment and survival of two temperate reef fishes: the bluebanded goby (*Lythrypnus dalli* Gilbert) and the blackeye goby (*Coryphopterus nicholsii* Bean). Shelter was manipulated by creating isolated 1-m^2 reefs that were composed of three densities of rocks (16, 32 and 64 rocks/m^2), which both species of goby used for shelter. A preliminary set of experiments done on reefs exposed to predators revealed that recruitment and survival of both fishes were positively affected by the density of rocks. The main set of experiments revealed the proximate causes of these effects of shelter. Replicate reefs of all three shelter treatments were either kept free of predators (enclosed in predator-exclosure cages) or exposed to predators (enclosed in partial cages). In *Coryphopterus*, survival and recruitment varied among shelter treatments on reefs exposed to predators, but not on reefs free of predators. This result indicates that shelter influenced the density of *Coryphopterus* by altering the impact of predators, thus supporting the prevailing hypothesis. In contrast, the effects of shelter on *Lythrypnus* were not caused solely by altering the impact of predation: survival and recruitment both varied among shelter treatments even when predators were absent. For survival of *Lythrypnus*, differences among shelter treatments were larger on reefs exposed to predators than on reefs free of predators, indicating that shelter did also modify the impact of predation. However, recruitment of *Lythrypnus* was affected similarly by shelter treatments regardless of whether predators were present or absent. Therefore, the effects of shelter were not caused by altering the impact of predators, and instead, it appeared that recruits responded directly to the abundance of shelter. These results indicate that for some reef fishes, positive relationships between abundance and shelter may not be caused by lower rates of predation in areas with

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abundant shelter. Instead, such relationships between abundance and shelter may be driven by prey preferences (exerted at or after the time of settlement) for areas with abundant shelter, or by use of shelter sites for purposes other than refuge from predators. Therefore, in the absence of any other evidence supporting a role of predation, positive relationships between the density of reef fishes and the abundance of shelter should not be construed as proof of the importance of predation in determining the abundance of reef fishes.

1. Introduction

A variety of factors have been shown to influence the spatial and temporal patterns of abundance of reef fishes (reviewed in Ebeling and Hixon, 1991; Jones, 1991; Sale, 1991; Caley et al., 1996). Amongst these factors is microhabitat, in particular, physical structures that may provide shelter from predators (e.g., corals, rocks and marcroalgae). A number of studies, both correlative (e.g., de Boer, 1978; Luckhurst and Luckhurst, 1978; Roberts and Ormond, 1987; Connell and Jones, 1991; Anderson, 1994; Carr, 1994; Tupper and Boutilier, 1997) and experimental (e.g., Shulman, 1984; Behrents, 1987; Hixon and Beets, 1989, 1993; Connell and Jones, 1991; Buchheim and Hixon, 1992; Carr, 1994; Caley and St. John, 1996), have detected strong influences of shelter availability on reef fish abundance. For clarity, I define a shelter site as a physical structure that an animal uses when predators are nearby, presumably to avoid predation. Since, by this definition, shelter sites are used by prey fishes in response to predators, it is reasonable to postulate that strong relationships between shelter and reef fish abundance (noted above) are caused by a negative relationship between the risk of predation and the availability of shelter. Indeed, this is the most prevalent hypothesis for such relationships, and so, studies detecting these sorts of relationships are usually interpreted as providing evidence for the important role of predation in structuring populations of reef fishes.

This interpretation of positive relationships between the abundance of reef fishes and shelter are bolstered by a growing body of experimental evidence that demonstrates strong effects of predators on the abundance of reef fishes (Doherty and Sale, 1985; Caley, 1993; Carr and Hixon, 1995; Steele, 1996, 1997a; Beets, 1997; Beukers and Jones, 1997). These studies have manipulated the density of predators directly, either by removal or with exclosure cages, to provide evidence of the important role of predation. Shelter however, may affect population density (and hence, species diversity: e.g., Hixon and Beets, 1989, 1993; Caley and St. John, 1996) in ways that are unrelated to reducing the impact of predation. As noted by many workers who have detected positive relationships between the density of reef fishes and the abundance of shelter, shelter sites may be used for purposes other than hiding from predators. For example, sites used to hide from predators may also be used as nest sites, as foraging sites, or as sites that provide refuge from harsh abiotic conditions, e.g., wave surge. Sites that serve these other purposes may also be limited, and therefore, population densities may respond to

the availability of shelter for reasons unrelated to predation. For example, Breitburg (1987) and Lindström (1988) have shown that numbers of nesting, male gobies increase rapidly after the addition of new nest sites to natural areas. Additionally, relationships between population density and the abundance of shelter may exist even in the absence of contemporary predation if a preference for areas with abundant shelter has evolved due to effects of predators over an evolutionary time scale (Bell and Westoby, 1986).

In this study, the proximate causes of positive relationships between the density of reef fishes and the availability of shelter were evaluated experimentally. Field experiments were first used to demonstrate positive effects of shelter availability on recruitment and survival of two species. After detecting such effects, a second set of experiments were conducted, which manipulated both shelter and predator-exposure orthogonally. This set of experiments revealed whether the relationships between fish density and shelter were driven entirely by shelter altering the rate of predation, or whether shelter had effects that were unrelated to altering the impact of predation.

2. Methods

2.1. Study system

This work was conducted at Santa Catalina Island, USA (33 27 N, 118 29 W) and focused on two abundant reef fishes, both members of the family Gobiidae. The bluebanded goby (*Lythrypnus dalli* Gilbert) is a small [< 49 mm standard length (SL)], brightly colored, active species that usually perches on rocks and mainly forages on zooplankton by briefly darting into the water column (Behrents, 1989). The blackeye goby (*Coryphopterus nicholsii* Bean) is larger (up to at least 90 mm SL), cryptic, less active, and normally rests on sand or rocks and forages on both benthic invertebrates and zooplankton. Both species use rocky crevices and overhangs for shelter and as nest sites (males guard demersal eggs attached to hard substrate until they hatch). The pelagic larvae of the two gobies eventually settle out of the plankton and into the same microhabitats used by juveniles and adults (i.e., there are no ontogenetic niche shifts in habitat use).

Other studies have demonstrated that predators can have considerable impacts on both recruitment and survival of the two goby species (Steele, 1996, 1997a,b, 1998; Steele et al., 1998), however these effects are spatially and temporally variable. At Santa Catalina Island, the primary predator of the two gobies is the kelp bass (*Paralabrax clathratus* Girard; family Serranidae), which comprises about 90% of all piscivorous predators at the island. In sandy areas, such as the site where the experiments were conducted, a less common serranid, the barred sand bass (*Paralabrax nebulifer* Girard) may also exert considerable predation pressure (Wiley, 1973). Due to their small size at settlement (*Lythrypnus*: 9–11 mm SL; *Coryphopterus* 15–25 mm SL), young individuals of both species may also be at risk of predation from some generalist microcarnivores, particularly the abundant rock wrasse (*Halichoeres semicinctus* Ayres).

2.2. Experiments

2.2.1. General description

Three experiments were conducted, all at Big Fisherman Cove on the protected north side of the island. The cove contains a variety of habitats, including kelp beds, reefs with only low-lying marcroalgae, and sandy areas. I constructed a grid of 1-m^2 replicate reefs built of rocks translocated from a large reef; treatments were assigned randomly to the reef positions. Reefs were separated from each other and from natural reefs by 10 m of sand bottom, which effectively precludes movement of the two goby species among reefs (Steele, 1997a,b). Experiments focused on two demographic responses to shelter and predation: survival and recruitment. To examine survival, a standard number of fish (see descriptions of particular experiments for details), which were marked subcutaneously with non-toxic acrylic paint, were stocked on each experimental reef. The acrylic marks allowed experimental fish to be distinguished from recruits that had settled from the plankton and from larger fish that had immigrated from large natural reefs in the cove (immigration from these reefs was rare). Because the two goby species rarely move among reefs separated by 10 m of sand bottom, I equate loss of marked fish from the experimental reefs with mortality. Recruitment was defined operationally as the accumulation of settlers from the plankton over 9–45 day periods that survived to be collected by divers. Hence, recruitment is a product of processes acting before, during, and after settlement. At the end of the experimental periods, recruits and/or surviving marked fish were collected by scuba divers using handnets and the anesthetic quinaldine (a 10% solution in 95% ethanol). Separate sub-experiments on recruitment and survival were conducted, i.e., recruitment was measured only during periods when older acrylic-marked gobies were not present on reefs, because older resident gobies may influence the recruitment of juveniles (Steele, 1997a).

In each experiment, three shelter treatments were used: low, medium and high. These treatments consisted of 16, 32 or 64 rocks ranging in length from 5–30 cm and of a uniform distribution of sizes (within and among treatments). The rocks were arranged on the sand bottom in a single layer over a 1×1 m area in a roughly uniform distribution. In the low-shelter treatments there were relatively large patches of sand between rocks, while in the high-shelter treatments, sand patches were small and many rocks were in contact with others. These experimental reefs effectively mimicked rubble patches occurring on natural reefs.

2.2.2. Effects of shelter: experiments 1 and 2

Two experiments were conducted to determine the effects of the availability of shelter on recruitment and survival of the two goby species: experiment 1 (June–September 1993) and experiment 2 (June 1994). Experiment 1 evaluated the effects of shelter on both recruitment of juveniles and survival of older gobies, while experiment 2 examined only recruitment. Experiment 2 was conducted in hopes of getting greater recruitment than in experiment 1 (particularly for *Lythrypnus*) to allow stronger statistical tests for effects of shelter. During both experiments, the three shelter treatments described above were used and all of the experimental reefs were exposed to predators (i.e., no cages were used).

During experiment 1, recruitment was measured over three non-overlapping periods, 18–45 days long. The total number of recruits, summed over these three periods, was used as the measure of recruitment during the experiment. Each of the three shelter treatments was replicated five times. Survival during experiment 1 was measured by stocking 10 *Coryphopterus* (16–35 mm SL, ranging from newly settled to about 1.5 mo post-settlement) and 10 *Lythrypnus* (17–37 mm SL, ranging from about 1 mo to 1 + yr post-settlement) on each reef simultaneously (i.e., 20 acrylic-marked fish/reef). Surviving gobies were collected after five days. The distribution of sizes of each goby species was equivalent among reefs (i.e., approximately the same mean and range of lengths on each reef). Survival was estimated with one fewer replicate per shelter treatment, i.e., $n = 4$. During experiment 2, only recruitment was measured and the experiment lasted only nine days. Replication was greater during experiment 2: $n = 8$ per shelter treatment.

2.2.3. Effects of shelter and predation: experiment 3

To test for effects of shelter that were independent of reducing predation, experiment 3 was conducted (June–August 1994). In this experiment, the same three shelter treatments were used but these were crossed with two levels of exposure to predators: + predators (+ P) and − predators (−P) (for each shelter/predation treatment combination, $n = 4$; $N = 24$). If shelter availability influences survival (or recruitment) only by altering risk of predation (i.e., shelter sites = refuge sites, and they serve no other purpose), then survival (or recruitment) should differ among shelter treatments on the + P reefs, but not among shelter treatments on − P reefs. If shelter has effects that are independent of providing refuge from predators, then even on the − P reefs there should be differences among shelter treatments.

Exposure to predators was manipulated with cages. − P reefs were enclosed in predator-exclosure cages that were $1 \times 1 \times 0.6$ m high, and built of 19-mm mesh, rigid plastic netting on a frame of PVC pipe (13 mm inner diameter). Nineteen-mm mesh does not hinder the movement of either goby species through cage walls and it is effective at keeping all fishes > ca. 80 mm SL out of caged areas. However, in other studies (e.g., Steele, 1997a, 1998), small (< 80 mm) piscivorous kelp bass sometimes managed to squeeze through the netting and invade exclosure cages. During the present study, small predators were never seen inside the exclosure cages. Because *Lythrypnus* is susceptible to artifacts of caging (Steele, 1996), the caged reefs were not compared to totally uncaged reefs, instead, they were compared to reefs in otherwise identical cages that lacked netting on one half of one side of the cage. These partial cages (+ P) do not differ from exclosure cages in their effects on the two goby species, and therefore, can provide unconfounded tests for effects of predators on the gobies (Steele, 1996).

During this experiment, recruits were collected three times, after being allowed to accumulate for periods of 9–25 days. As in experiment 1, the sum of recruitment during the three periods was used as the measure of recruitment during the experiment.

To test for effects of shelter and predation on survival of the two goby species, two separate sub-experiments were run: one with *Coryphopterus* and one with *Lythrypnus*. In each case, 10 acrylic-marked fish were stocked on each reef and survivors were collected after two days (*Coryphopterus*: 10–12 July) or five days (*Lythrypnus*: 1–6 August). Fish used in this experiment were similar in size and age to those used in

experiment 1, ranging in length from 19–33 mm SL for *Coryphopterus* and 16–34 mm SL for *Lythrypnus*. An equivalent distribution of sizes was stocked on each reef.

2.2.4. Statistical analyses

Tests for effects of shelter and predation were made with analysis of variance (ANOVA). For experiments 1 and 2, one-way ANOVA was employed to test for differences among the three shelter treatments. For experiment 3, two-way ANOVA was used to test for main effects of shelter and predation and for an interaction between the two factors. Additionally, separate one-way ANOVAs, for each of the two predator-exposure treatments, were also used to clarify the existence and cause of shelter effects. If differences among shelter treatments are caused by altered rates of predation among treatments and nothing else, then survival and recruitment should vary among shelter treatments on reefs exposed to predators (+ P reefs), but not on reefs free of predators (−P reefs). Given sufficient statistical power, such a difference in the pattern of response to shelter between the two predation treatments should be indicated by a significant interaction between shelter and predation. However, a significant interaction between shelter and predation in a two-way ANOVA does not demonstrate that differences among shelter treatments occurred only in the presence of predators (+ P reefs). For example, the magnitude of differences among shelter treatments on reefs free of predators simply may not be as large as those differences on reefs exposed to predators, and this may cause a significant interaction. Moreover, even when the hypothesis that effects of shelter occur only in the presence of predators is true, this hypothesis may not be supported by a statistically significant interaction between shelter and predator-exposure because the power of tests for interactions is inherently low (i.e., compared to tests of main effects: Winer et al., 1991). For the reasons listed above, using two separate one-way ANOVAs for an experiment often helped to clarify differences in responses to shelter between predation treatments. For any analysis, where necessary to satisfy the assumptions of normality and homoscedasticity, data were appropriately transformed (see Section 3 and pertinent tables for details).

3. Results

3.1. Effects of shelter: experiments 1 and 2

Survival and recruitment of both goby species increased with increasing availability of shelter. During both experiments 1 and 2, recruitment of *Coryphopterus* increased significantly with increasing shelter [Figs. 1A and B; one-way ANOVA: experiment 1: $F_{2,12} = 23.0$, $P = 0.0001$; experiment 2 {data transformed to $\ln(x + 1)$}: $F_{2,21} = 19.1$, $P = 0.00002$). *Lythrypnus* did not recruit during experiment 2, but during experiment 1, recruitment of this species also increased with increasing availability of shelter (Fig. 1C). However, when tested with ANOVA, differences in recruitment of *Lythrypnus* among shelter treatments were not significant ($F_{2,12} = 1.60$, $P = 0.24$), presumably due to low power (power to detect these differences with $= 0.05$ was only 28%). Very few *Lythrypnus* recruited – 16 total – and recruitment was quite variable among replicates.
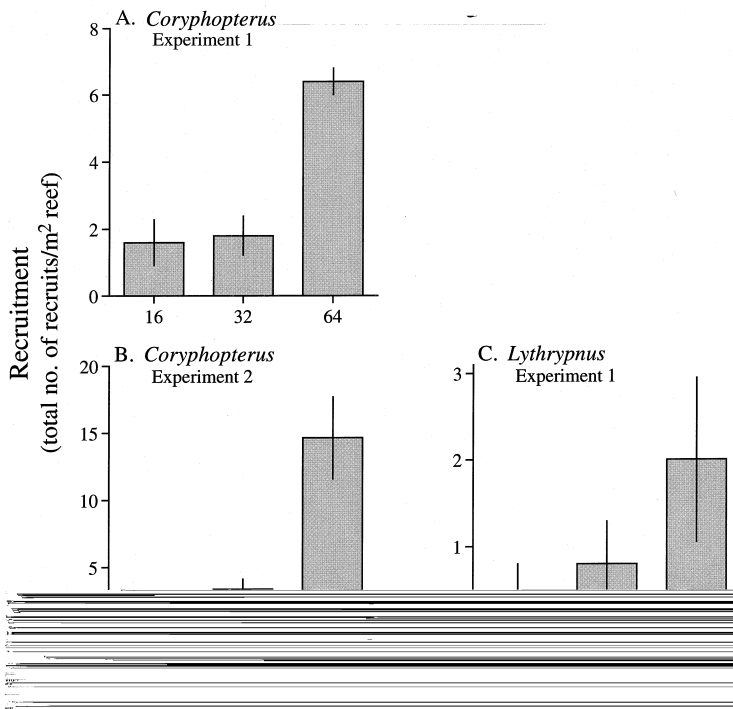
Fig. 1. Effects of the availability of shelter (in the presence of predators) on recruitment of the two goby species. Error bars represent 1 S.E.; $n = 5$ for each bar, except for experiment 2, where $n = 8$. See Section 3.1 for pertinent statistical tests.

But when the total number of recruits was pooled within each treatment and differences among treatments tested with a x^2 test, differences were significant ($x^2 = 6.50$, df $= 2$, $P < 0.05$).

Survival of both goby species also increased significantly with increasing shelter availability in experiment 1 [Fig. 2; *Coryphopterus*: one-way ANOVA: $F_{2,9} = 75.3$, $P = 0.000002$; *Lythrypnus*: Kruskal–Wallis non-parametric ANOVA (used because survival was zero in all replicates of the low-shelter treatment): $P = 0.012$].

3.2. Effects of shelter and predation: experiment 3

The causes of effects of shelter availability differed between the two goby species. The effects of shelter on *Coryphopterus* were mainly caused by shelter altering the impact of predation. In the presence of predators (+ P reefs), recruitment of *Coryphopterus* tended to increase with increasing shelter availability (Fig. 3A; although differences among shelter treatments were not quite statistically significant: one-way ANOVA: $F_{2,9} = 3.8$, $P = 0.06$). However, in the absence of predators (−P reefs), shelter availability had no effect on recruitment (Fig. 3A; one-way ANOVA: $F_{2,9} = 0.7$,
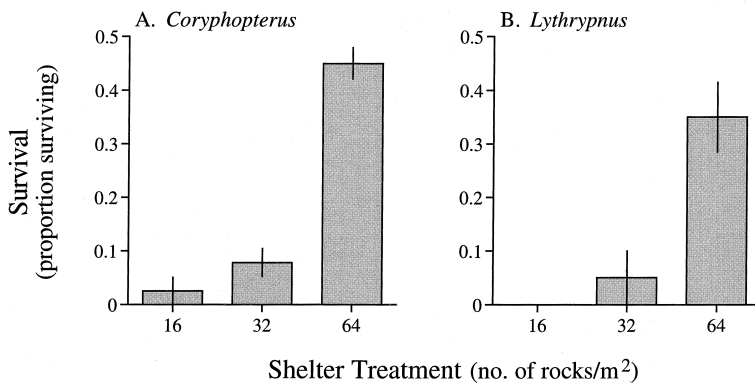
Fig. 2. Effects of the availability of shelter (in the presence of predators) on survival of the two goby species. Error bars represent 1 S.E.; $n = 4$ for each bar. See Section 3.1 for pertinent statistical tests.

$P = 0.5$). There was no statistically significant interaction between shelter availability and predation (Table 1), but the power to detect such an interaction was low (35%).

Similarly, survival of *Coryphopterus* was significantly influenced by shelter availability only in the presence of predators (Fig, 4A) (one-way ANOVAs: $+$ P reefs: $F_{2,9} = 9.8$, $P = 0.005$; $-$ P reefs: $F_{2,9} = 0.3$, $P = 0.7$). However, there was no interaction between shelter availability and predation (Table 2), but, again, there was little power to detect this interaction (power $< 10\%$).

In contrast to *Coryphopterus*, recruitment and survival of *Lythrypnus* was influenced by shelter availability both in the presence and absence of predators. Recruitment of *Lythrypnus* increased with availability of shelter and this pattern did not differ between
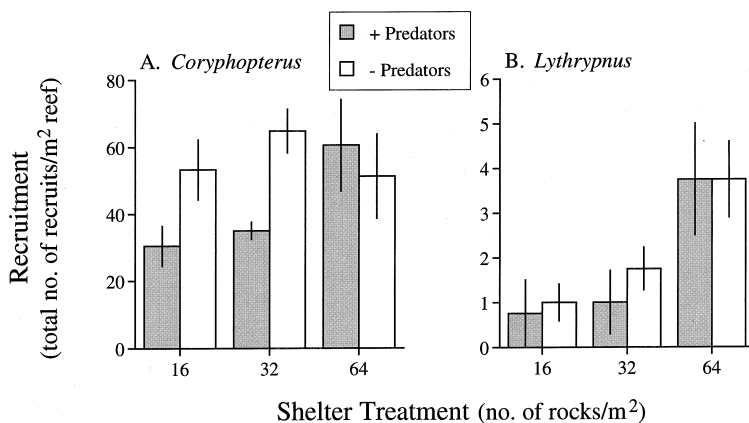

Fig. 3. Effects of the availability of shelter on recruitment of both goby species, both in the presence and absence of predators. Error bars represent 1 S.E.; $n = 4$ for each bar. See Table 1 Section 3.2 for pertinent statistical tests.

Table 1
Results of two-way ANOVA testing for effects of shelter and predation on recruitment of *Coryphopterus* and *Lythrypnus* (see Fig. 3)

Factor	SS	df	F	P
Coryphopterus[a]				
Shelter	0.36	2	1.30	0.30
Predation	0.65	1	4.61	0.046
Shelter × predation	0.81	2	2.90	0.081
Error	2.52	18		
Lythrypnus[b]				
Shelter	3.71	2	7.76	0.004
Predation	0.22	1	0.93	0.35
Shelter × predation	0.09	2	0.20	0.82
Error	4.30	18		

[a] Recruitment of *Coryphopterus* was transformed to $\ln(x + 1)$ to satisfy the assumption of homogeneity of variances.
[b] Recruitment of *Lythrypnus* was transformed to square $\text{root}(x + 0.5)$ to improve normality.

reefs with and without predators (Fig. 3B, Table 1). This indicates that effects of shelter availability on recruitment of *Lythrypnus* were completely unrelated to provision of refuge from predation. Survival of *Lythrypnus* also varied among shelter treatments in the absence of predators (one-way ANOVA: $F_{2,9} = 4.55$, $P = 0.04$), as well as in their presence (one-way ANOVA: $F_{2,9} = 16.0$, $P = 0.001$). However, the differences among shelter treatments were much greater on reefs exposed to predators (Fig. 4B) resulting in a significant interaction between shelter availability and predation (Table 2). So, for older and larger *Lythrypnus* (i.e., the acrylic-paint-marked fish), shelter did provide refuge from predators, but it also affected survival in ways independent of altering the impact of predation.

Table 2
Results of two-way ANOVA testing for effects of shelter and predation on survival of *Coryphopterus* and *Lythrypnus* (see Fig. 4)

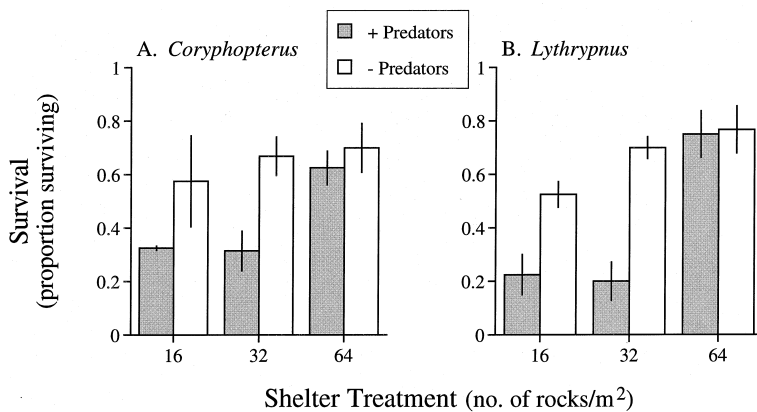| Factor	SS	df	F	P
Coryphopterus				
Shelter	0.20	2	2.93	0.079
Predation	0.31	1	8.91	0.008
Shelter × predation	0.08	2	1.12	0.33
Error	0.62	18		
Lythrypnus				
Shelter	0.66	2	16.59	0.0001
Predation	0.44	1	22.33	0.0002
Shelter × predation	0.24	2	5.93	0.010
Error	0.36	18		

Fig. 4. Effects of the availability of shelter on survival of both goby species, both in the presence and absence of predators. Error bars represent   1 S.E.; *n* = 4 for each bar. See Table 2 Section 3.2 for pertinent statistical tests.

4. Discussion

Recruitment and survival of both of the two reef fishes that I studied both increased as shelter increased (Figs. 1 and 2). However, the causes of the positive relationships between survival and recruitment were not the same for both species. For example, the abundance of shelter affected recruitment and survival of *Coryphopterus* only when predators were present (Figs. 3 and 4), indicating that shelter sites served this species primarily by providing refuge from predation. In contrast, the availability of shelter affected both recruitment and survival of *Lythrypnus* even when predators were absent (Figs. 3 and 4). This result indicates that the effects of shelter availability were not confined solely to altering the impact of predation by providing refuge from predators. The influence of such independent effects on recruitment of *Lythrypnus* were par- ticularly striking. The patterns and magnitude of recruitment among shelter treatments were virtually identical on reefs exposed to predators and on reefs protected from predators (Fig. 3B). This result suggests that the effects of shelter were not caused by altering the impact of predation. Variation in the survival of older *Lythrypnus* among shelter treatments appeared to be the combined result of altered rates of predation and other, independent, effects of shelter. The effects of altered rates of predation, however, were much greater than the other effects of shelter (Fig. 4B).

It is not clear why survival and recruitment of *Lythrypnus* increased with the availability of shelter where predators were absent. One unlikely possibility is that "predator-free" reefs (−P treatment) were not actually not free of predators. This could have occurred if small predators had managed to squeeze through the netting of the exclosure cages. This actually occurred in another experiment conducted a year earlier at the same site (Steele, 1997a). During that experiment, small kelp bass (< 80 mm SL) invaded exclosure cages and took up residence on experimental reefs. However, during

the present study, small predators were never seen inside the exclosure cages, so I am confident that ''predator-free'' reefs were truly free of predators.

Other possible causes of the positive effect of shelter found in the absence of predators include the use of shelter sites for shelter from wave surge, use as nest sites, or an evolved preference for areas with abundant shelter. Although the importance of shelter from surge cannot be completely discounted (and it may be of particular importance during stormy winter months and at sites with high wave energy), it seems unlikely to have been the cause of the positive effect of shelter found in the absence of predators during the present study for two reasons. (1) The study site is located in a calm area that was exposed to very little surge during the experiments, and (2) both goby species should have been influenced similarly by this factor (and they were not). Likewise, as a proximate explanation for the positive effect of shelter found on reefs free of predators, nest-site limitation during the present study seems unlikely. The strongest evidence against limitation of nest sites is that the largest effects of shelter that were found in the absence of predators occurred in young *Lythrypnus* recruits. None of these recruits were old or large enough to breed and, hence, had no immediate need of a nest site. (Notably, Breitburg (1987) found that nest sites were a limited resource for adult male *Coryphopterus nicholsii*. *C. nicholsii* used in this study, however, were all immature and hence needed no nests, but later in life, the density of nest sites may limit the density of this species).

If shelter sites are important for any of the reasons listed above (i.e., refuge from predators, shelter from surge, nest sites), then it is reasonable to expect that preferences for areas with abundant shelter should evolve. Such preferences may be manifest at the time of settlement and/or later in life, when fish may abandon areas where shelters are rare in search of areas where shelters are more abundant. Many reef fishes are capable of choosing particular microhabitat types at settlement (e.g., Sweatman, 1983, 1985, 1988; Booth, 1992; Wellington, 1992; Tolimieri, 1995) and in some cases, preferred sites confer greater post-settlement survival (e.g., Forrester, 1990; Wellington, 1992; Booth, 1995). Preferences for areas with abundant shelter may also be exercised after settlement, and this could reduce survival in areas with relatively few shelters. These sorts of effects on survival could occur if areas with relatively few shelters are separated from areas with more abundant shelter by zones with very little or no shelter. In this scenario, migration across areas with very little shelter (e.g., sand) in search of areas with abundant shelter would entail an elevated risk of predation. Such spatial arrangements of areas varying in the availability of shelter certainly occur in systems where patch reefs are common, and also occur, to a lesser extent, on large tracts of continuous reef. On the grid of isolated, experimental reefs used in this study, where reefs were separated by a minimum of 10 m of sand, movement across these sandy expanses entails a high risk of predation (personal observations). In this situation, a behavioral decision to abandon areas with little shelter, based on an evolved preference for areas with abundant shelter, could have generated the positive relationship between survival and the availability of shelter found on predator-free reefs in *Lythrypnus*.

Evolved preferences for areas with abundant shelter may be largely responsible for the positive effects of shelter availability on recruitment and survival of *Lythrypnus*. But why such preferences were not manifest in *Coryphopterus* on predator-free reefs is

puzzling. There should be strong selective pressure for this species to evolve preferences for areas with abundant shelter, given that its survival was strongly affected by the abundance of shelter when exposed to predators. Oddly, both Connell and Jones (1991) and Tupper and Boutilier (1997), working with two temperate reef fishes, found a similar lack of preference at settlement for habitats that conferred greater post-settlement survival. Both pairs of authors suggested that shelter for newly settled fish may actually be equivalent among habitats that vary in post-settlement survival, but that settlers rapidly outgrow the abundant small shelters and then suffer greater predation in habitats with limited shelter suitable for larger fish. Even so, there should still be strong selection for the evolution of settlement preferences for areas that provide abundant shelter for older stages. Perhaps settling larvae of these three species are just incapable of distinguishing between areas of high vs. low shelter.

The present study was conducted on small, isolated, artificial reefs. This approach allowed survival and recruitment to be estimated with little worry of confounding these rates with migration (which would be much more likely on large, continuous, natural reefs). The effects of predators were tested by manipulating predator abundance with cages, which was the only feasible way to manipulate the mobile predators that are common at the study site. These methods, however, may limit the extent to which one can extrapolate the findings of this study to more natural circumstances. For instance, it is difficult to know whether rates of predation that are measured on small artificial reefs are representative of rates of predation occurring on large tracts of continuous reef. On one hand, predators may aggregate to small isolated habitat patches, which could cause rates of predation to be unnaturally elevated. But, on the other hand, there may be fewer predators in the vicinity of isolated habitat patches, which could reduce rates of predation. Hence, it is hard to predict whether the rates of predation measured on small isolated reefs, like those used in this study, are greater than, less than, or the same as those occurring on natural reefs.

Another factor that makes it difficult to predict how well the rates of predation that were measured in this study correspond to those on natural reefs is how the effects of predators were tested. Comparing partially-caged reefs with completely-caged reefs may have biased estimates of predation. Steele (1996) has discussed this issue in detail for the same species, cages and reefs used in the present study. Briefly, partial cages may attract predators [though the evidence for this, in this particular system, is not strong (Steele, 1996)], which could elevate the rate of predation on partially-caged reefs. However, this potential increase in the rate of predation may be offset by reduced efficacy of predators on partially-caged reefs because the structure of the partial cage may interfere with the foraging tactics of the predators. In fact, Steele (1996) concluded that by comparing partially-caged reefs with completely-caged reefs the true impact of predation on *Coryphopterus* was underestimated.

In addition to influencing the behavior of predators, cages may influence the behavior of prey. However, by comparing partial cages with complete exclosure cages, which were very similar to one another, this problem was largely avoided (Steele, 1996). Nonetheless, the presence of either structure (partial or complete cages) could influence the recruitment of goby larvae. If artifacts of caging influence the density of recruits, this could bias the estimate of the impact of predation, if, for example, predation is

density-dependent. Settling fish larvae may be attracted or repelled by the structure of cages. However, in fact, there is little evidence for artifactual effects of caging on recruitment of either goby species used in the present study. Steele (1997a) found that recruitment of *Lythrypnus* did not differ significantly between partially-caged (same design as the present study) reefs and uncaged reefs (mean number of recruits/m^2 1 S.E.: 10.0 3.1 vs. 7.0 1.8, for partially-caged reefs and uncaged reefs, respectively). And making the same comparison for *Coryphopterus*, Steele et al. (1998) found no effect of the partial cages (mean number of recruits/m^2 1 S.E.: 1.7 0.5 vs. 1.9 0.5, for partially-caged reefs and uncaged reefs, respectively). So overall, there appeared to be no major artifacts of the cage structures on recruitment of the two goby species. However, because of potential effects of the partial cages on the behavior of predators, and the use of small isolated patch reefs, it is difficult to predict how easily the results of this study can be extrapolated to other, more natural situations.

However, within the context of the experimental system used, this study clearly demonstrates that the availability of shelter can influence the abundance of reef fishes even when predators are absent. This result indicates that studies that find positive relationships between the density of reef fishes and shelter should not be interpreted (as they sometimes have been) as demonstrating an ecologically important role of predation in determining patterns of abundance. Direct tests of the effects of predation must be made to determine its importance. The finding that the availability of shelter influenced the recruitment of one reef fish (*Lythrypnus*) without altering rates of predation, does not discount the potential importance of predators. Indeed, predation was found to affect both fish species in this study, and these effects of predators sometimes interacted with the effects of shelter. Moreover, predators may ultimately be responsible for causing an evolutionary preference for areas with abundant shelter. This preference alone could cause positive relationships between the abundance of reef fishes and shelter.

In conclusion, there is widespread evidence for a strong relationship between the abundance of reef fishes and the abundance of shelter. A more complete understanding of the underlying causes of this relationship (e.g., current predation vs. evolved habitat preferences) will enable us to better predict the causes of spatial and temporal variation in the abundance of reef fishes. In particular, such an understanding will help us to predict how populations of reef fishes will respond to events that alter the availability of shelter (e.g., storms or warm-water events that reduce the abundance of corals or macroalgae that are used as shelter).

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