

Settling larvae of a small coral-reef fish discriminate reef features at large, but not small, spatial scales

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Abstract

Larval settlement of a small coral-reef fish, the bridled goby (*Coryphopterus glaucofraenum*), to five entire reefs over 4 yr decreased with increasing cover of hard substrate (rock and coral). Experimentally increasing rock cover on these large reefs caused a reduction in settlement that lasted 3 yr, confirming that settling coral-reef fish discriminate among sites at the mesoscale (hundreds of meters to tens of kilometers). Counterintuitively, a small-scale manipulation of rock cover and an observational study both suggest that settlers show no response to rock cover at the microscale (few to tens of meters). Habitat selection at settlement can, thus, set initial benthic population size at much larger spatial scales than previously recognized, a finding consistent with the good swimming and sensory capabilities of late-stage larvae.

Most benthic marine invertebrates and fishes have a pelagic larval stage. How these larvae colonize suitable adult habitats is critical to understanding their evolution, population biology, and community dynamics (Caley et al. 1996). The rate at which larvae become established in benthic habitats, a process referred to as settlement, shows clear spatial patterns at domains ranging from centimeters to hundreds of kilometers in extent (Doherty 1991). It is well-known that settling larvae can select specific habitats at microscales, over distances from a centimeter to a meter, (review by Kingsford et al. 2002). Experiments have revealed that larvae choose sites according to a variety of physical attributes (Sale et al. 1984; Butman 1987), some of which arise from the presence of conspecifics (Knight-Jones

1953) or other species (Sale et al. 1984). Related research has identified a variety of chemical, auditory, visual, and other cues that larvae use to make these finely resolved choices about where to settle (review by Kingsford et al. 2002).

It has generally been assumed that patterns of settlement at mesoscales (hundreds of meters to tens of kilometers) and upwards are created by processes that transport or retain larvae in the pelagic realm, and ultimately bring them to the vicinity of adult habitats (Shanks 1995; Kingsford et al. 2002). Supporting this hypothesis is evidence that oceanographic features can transport larvae and deliver them close to settlement sites (Pineda 1991). Moreover, mesoscale variation in the density of recently settled individuals is sometimes correlated with variation in physical transport (Shanks and Wright 1987).

The larvae of fish and most invertebrates are, however, not passive particles at the mercy of currents. Common larval behaviors, especially vertical migration (Young and Chia 1987), can position larvae in water masses favoring either horizontal movement (DiBacco et al. 2001) or stationarity (Paris and Cowen 2004) depending on the species and context. Various lines of evidence indicate that settling larvae have the potential to select benthic habitats actively at mesoscales. Larvae of some coral-reef fishes, for example, seem able to position themselves near fore-reefs but avoid lagoons near the time of settlement, suggesting that mesoscale habitat selection can begin in the pelagic stage (Doherty et al. 1996). Mesoscale habitat selection is also implied by differences among sites in settlement despite homogeneity in the distribution of late-stage larvae (Doherty et al. 1996; Jenkins 2005). For larval reef fishes, the possibility for active choice among mesoscale sites is suggested by the strong swimming ability of late-stage

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larvae (Stobutzki and Bellwood 1997) and the fact that they can orient either to reefs themselves (Leis and Carson-Ewart 2003) or to chemical and auditory cues produced by reefs (Montgomery et al. 2006). Evidence is growing that larval fishes can detect the presence of reefs at distances from hundreds of meters to >1 km. The fact that some reef-fish larvae can recognize the smell of their natal reef (Gerlach et al. 2007) further suggests that natal homing (Jones et al. 1999) may result partly from active site selection at settlement.

Objectives and study species—To date, however, we are aware of no direct evidence for mesoscale habitat selection at settlement. Our objective in this study was to test whether settling reef fishes choose among large reefs based on specific attributes. We studied the bridled goby (*Coryphopterus glaucofraenum* Gill), which occupies coral reefs throughout the Caribbean. Bridled gobies release pelagic larvae that settle to reefs after about a month in open water (Sponaugle and Cowen 1994). Gobies are 6.5–8.0 mm standard length (SL; Sponaugle and Cowen 1994) at settlement, mature at 22–25 mm SL, and can reach ~55 mm SL, but they rarely live longer than a year (M. A. Steele and G. E. Forrester unpubl. data). After settlement, gobies occupy small home ranges up to a few square meters in area. These home ranges contain a mix of sand and hard substratum (scleractinian coral or rock) because gobies feed on meiofauna in the sand but, when threatened or attacked by predators, they seek refuge temporarily in small crevices at the edges of corals or rocks. An increase in the fraction of bottom covered by rock and coral means an increase in crevice density, up to a threshold of about 50% cover (Forrester and Steele 2004). Above this threshold, goby density declines, perhaps because there is not enough sand for foraging. Below 50% rock and coral cover, crevice density is important to adult gobies because they are killed primarily by predators, and their vulnerability is determined by the number of refuges in their home range (Forrester and Steele 2004).

We tested whether settling gobies choose reefs based on this important reef attribute—the percent cover of small rocks and corals. We tested whether settling gobies respond to rock and coral cover at two spatial scales: on entire reefs several thousand square meters in extent, and in small habitat patches a few square meters in area. We first asked whether settlement onto entire reefs is correlated with ambient rock and coral cover. Second, we manipulated rock cover on entire reefs to test directly for mesoscale habitat selection by settling fishes. Third, we asked whether settlement to small habitat patches is correlated with rock and coral cover. Finally, we created small habitat patches varying in rock cover to test experimentally for microscale habitat selection.

Methods

Is settlement correlated to rock and coral cover on entire reefs?—We tested for a large-scale correlation between goby settlement and the cover of rock and coral on five entire reefs near Lee Stocking Island, Bahamas

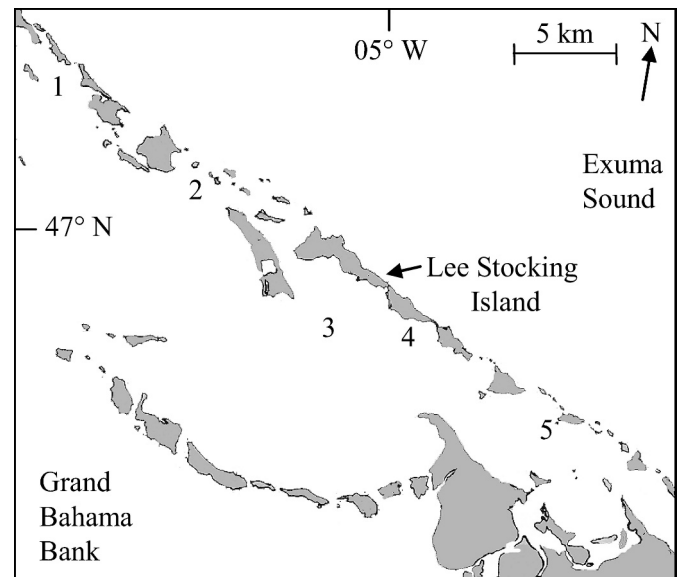


Fig. 1. Map showing the five entire reefs near Lee Stocking Island, Bahamas. The reefs are as follows: (1) Goby Spot, (2) Rainbow, (3) Tug and Barge, (4) Windssock, and (5) Square Rock.

(23°46'N, 76°10'W). These reefs are a mix of scleractinian corals, limestone rock, sand, and other sessile reef-dwelling organisms. Each reef contained 3500–15,000 m² of suitable goby habitat, and each was isolated from any other goby habitat by ≥150 m of sand. The reefs occur over a 25-km portion of the Great Bahama Bank (Fig. 1), close to the Exuma Cays, which separate the shallow sandy bank from the far deeper Exuma Sound. Settlement-stage fishes are transported from Exuma Sound to reefs on the bank through channels between the Cays, primarily on nighttime flood tides (Thorrold et al. 1994). Each year from 1998 to 2001, divers visually estimated the percent of the bottom covered by different substrata: live and dead scleractinian coral, rock, sand, sponges, soft corals, and other benthic organisms. At each reef, we estimated substratum cover in 25 1.5-m × 1.5-m plots. Replicate plots were placed at random locations within 10-m-long sections of reef, which were themselves spread evenly along the reef.

At each reef, we also measured settlement from 1998 to 2001. Because larval gobies, like most reef fishes, settle to reefs nightly over a long reproductive season (Jun through Sep at this site) and suffer intense mortality within the first few days of arrival, precise estimates of settlement require daily monitoring of newly settled fish. However, because daily monitoring would have been prohibitively labor-intensive on five entire reefs, we used a weekly sampling method that still provides a measure of settlement comparable to that obtained with daily sampling (Steele and Forrester 2002).

The duration and timing of sampling varied from year to year (duration: 7–12 weeks; start dates: 07 Jun–09 Jul; end dates: 23 Aug–07 Sep). Settlement was measured within five 1.5-m × 1.5-m plots at each reef, which were placed in a stratified random fashion as described above. The plots were unaltered, except that they were covered with a cage

(made from a polyvinyl chloride frame covered with 5-mm plastic mesh). The mesh was permeable to settling gobies, but excluded the larger fishes that prey on them. Previously, we found no evidence that these cages affect settlement (Steele and Forrester 2002). Divers collected and measured the newly settled gobies that accumulated on the plots each week. Gobies that had settled in the preceding week were distinguished from older residents by size (Steele and Forrester 2002). For statistical analysis, our unit of replication was the number of settlers collected from each plot each week, averaged over the summer.

We used analysis of covariance (ANCOVA) to test for a relationship between rock and coral cover and goby settlement. The ANCOVA model included terms for the effect of year (a categorical factor), rock and coral cover (a linear covariate), and their interaction.

Is settlement correlated to rock and coral cover on small habitat patches?—We next tested for a small-scale correlation between goby settlement and rock and coral cover using the five entire reefs near Lee Stocking Island, Bahamas. In 2001, we estimated the percent cover of coral, rock, and other substrata inside the five plots used to monitor settlement on each reef. These percent-cover estimates in settlement plots were separate from the estimates described above to characterize the entire reefs. With settlement plots as replicates, we used ANCOVA to test for an effect on settlement (averaged over the summer) of rock and coral cover (a linear covariate), site (a categorical factor), and their interaction.

Do settlers respond to manipulation of rock cover on entire reefs?—To test directly for a mesoscale effect of rocks on larval settlement, we next manipulated the cover of rock on our five Bahamian reefs. Each reef was divided in half, and one half (50% of the reef area, ~1800–8000 m²) was selected at random for an increase in rock cover, while the half remained unaltered as a control. The rock-addition treatment was staggered over 3 yr. Rock was added to Square Rock and Tug and Barge in 2003, to Goby Spot and Windsock in 2004, and to Rainbow in 2005. Rocks were added to the first four reefs in mid-June and to Rainbow Reef in early July. To add rock, we took advantage of the abundant limestone rock (10–50 cm in diameter) that occurs naturally on local beaches. Rock was distributed over each reef by boat, and later rearranged by divers to produce relatively even coverage. The initial rock addition took 7 d reef⁻¹ on average, and some additional rock was added to three of the sites (Goby Spot, Square Rock, and Windsock) in late July 2004.

Divers made visual estimates of the percent cover of rock, coral and other substrata in 4-m × 4-m plots on each reef. Eight plots were sampled on the control side and eight on the experimental side of each reef. We made repeated estimates in case storms, or burial under sand, altered rock cover. Estimates were made in June and November 2003, in October 2004, and in August and October 2005. To assess the effectiveness of rock addition, we used a paired *t*-test to test the null hypothesis of no difference between the control and experimental halves of each reef. Separate tests were

performed on data collected before and after the manipulation.

We monitored goby settlement to the reefs through the summers of 2003–2005, using procedures identical to those employed in 1998–2001. We monitored five plots on the control half of each reef and five plots on the treatment half. In 2003 and 2004, we started monitoring settlement in late June, within a week of completing the rock addition. In 2005, however, we started monitoring settlement in mid-June but, because the rock addition at Rainbow reef was performed in early July, settlement at Rainbow in 2005 was monitored for 4 weeks before rock addition and for 7 weeks afterwards. Our unit of replication was the settlement rate on one side of a reef averaged over the summer, except for Rainbow in 2005 where separate averages were calculated for the pre- and post-manipulation periods. Effects of rock addition were assessed using paired *t*-tests, as described above for percent cover estimates.

Do settlers respond to manipulation of rock cover on small habitat patches?—The final component of our study was a manipulation of rock cover in small units of habitat. The design of this experiment was influenced by a possible artifact in the previous large-scale manipulation. Increasing rock cover by using limestone rubble from the beach raised the possibility that something related to the terrestrial origin of the rock, rather than rock cover itself, might influence goby settlement. Consequently, we used an ANCOVA design for the small-scale experiment to isolate the effects of the categorical factor rock type (beach rock vs. submerged rock from nearby reefs) and the linear covariate rock cover (each replicate patch contained a different number of rocks).

This experiment was done on 16 replicate habitat patches built in a sandy bay, 6–8 m deep, on the southern leeward side of Guana Island, British Virgin Islands (64°35'W, 18°29'N). Reefs in this area are generally similar to our Bahamian sites in goby density, substratum composition, and the community composition of other fishes (Steele and Forrester 2002; Forrester and Steele 2004). The patches were separated by ≥7 m of sandy substratum from each other, and from any natural reef. Each patch was circular (8–12 m² in area), and consisted of small piles of rubble (10–40 cm diameter) placed on the sand. Rock cover was varied by using different amounts of rubble to make each patch. Eight of the patches were built of coral rubble collected from a nearby reef (reef rock) and the other eight were built using limestone from nearby beaches (beach rock). The patches were constructed from 02 August to 06 August 2006, and goby settlement was monitored for the following 21 d (07–27 Aug 06). Each day, between 08:30–10:30 h, two divers independently searched each patch, plus the area within 1.5 m of its edge, and removed all settlers encountered.

Results

We collected 5624 goby settlers on the five entire reefs from 1999 to 2001. These gobies settled at significantly lower rates on reefs with more rock and coral (ANCOVA:

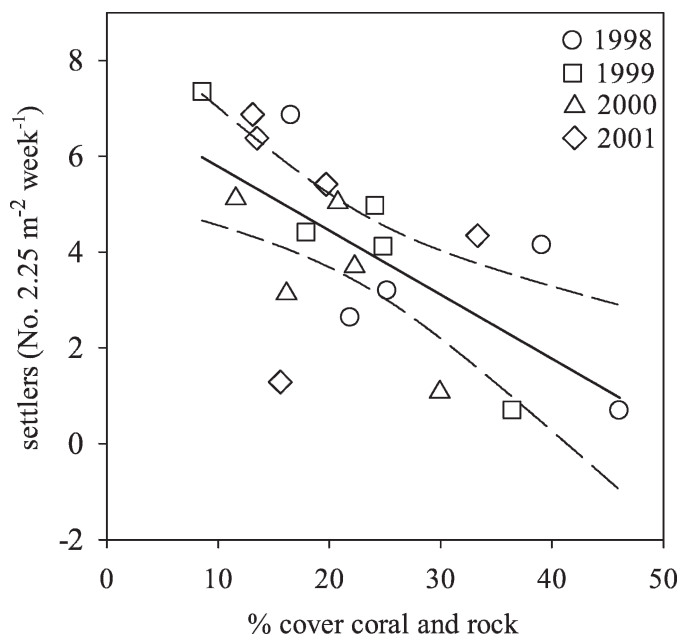


Fig. 2. Large-scale association between settlement and rock and coral cover of five large natural reefs. Data are plotted for each of 4 yr (1998–2001) showing the results of a linear regression ($\pm 95\%$ confidence interval [CI]) fit through all of the data. See text for details of statistical analysis.

$F_{1,15} = 11.78$, $p = 0.004$; Fig. 2), and this relationship did not differ demonstrably in either slope (ANCOVA: $F_{4,15} = 0.55$, $p = 0.700$; Fig. 2), or elevation (ANCOVA: $F_{4,15} = 1.79$, $p = 0.704$; Fig. 2) among the 4 yr of observation.

We collected 2480 goby settlers on the five entire reefs in 2001. The rate at which these gobies settled to small habitat patches within the reefs was unrelated to the cover of rock and coral within the patch (ANCOVA: $F_{1,15} = 0.554$, $p = 0.468$; Fig. 3). There was also no indication that the patch-scale relationship between settlement and habitat differed among reefs (ANCOVA: $F_{4,15} = 0.425$, $p = 0.789$), nor was there any demonstrable difference in settlement rates among reefs (ANCOVA: $F_{4,15} = 1.129$, $p = 0.380$). The lack of correlation between goby settlement and substrate composition at this small spatial-scale stands in contrast to the negative correlation observed among entire reefs.

We collected a total of 5624 newly settled gobies during our manipulation of rock cover on entire reefs. Control and treatment sections of the reefs were similar in percent rock cover before rocks were added (mean = 6.8% and 7.0% respectively; paired t -test: $t = -0.11$, $df = 5$, $p = 0.915$; Fig. 4). After the manipulation, however, rock cover in the treatment areas (mean = 10.2%) was more than double that in the control areas (mean = 4.0%; paired t -test: $t = 4.52$, $df = 10$, $p = 0.001$; Fig. 4). Not surprisingly, adding rocks had very little influence on live coral cover (Fig. 4). Control and manipulated areas were similar in live coral cover (mean = 2.2% and 3.3% respectively) before the manipulation (paired t -test: $t = -1.15$, $df = 5$, $p = 0.299$) and, the same was true after the manipulation (control

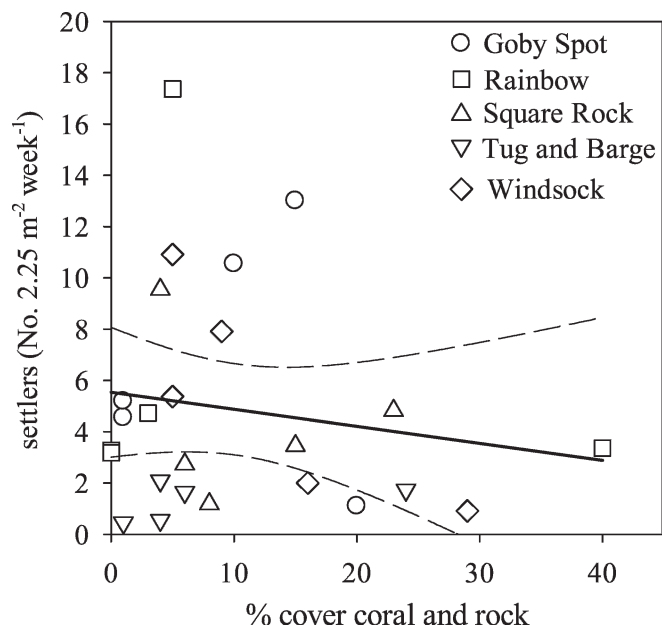


Fig. 3. No correlation between rock and coral cover and settlement on small habitat patches. Five patches were monitored within each of five large reefs during 2001. Plotted are the results of a linear regression ($\pm 95\%$ CI) fit through all of the data. Details of statistical analysis are described in the text.

mean = 3.6%; experimental mean = 4.7%; paired t -test: $t = -1.39$, $df = 10$, $p = 0.193$).

Settling gobies showed no obvious preference for control or experimental half of a reef prior to the manipulation (paired t -test: $t = 0.475$, $df = 4$, $p = 0.456$; Fig. 4). Mean settlement (number of settlers $2.25 \text{ m}^{-2} \text{ week}^{-1}$) in the control (4.70) and treatment halves (4.14) of a given reef differed on average by only 5.6%. After the manipulation, however, there was a strong bias against the experimental sections of reef. Gobies settled at much lower rates in the rock-addition areas (2.49 settlers $2.25 \text{ m}^{-2} \text{ week}^{-1}$) than in control areas (3.99 settlers $2.25 \text{ m}^{-2} \text{ week}^{-1}$). On a given reef, gobies settled at a 68.2% lower rate on the rock addition side than on the control side (paired t -test: $t = 3.66$, $df = 10$, $p = 0.004$; Fig. 4). The results of the experiment are, therefore, consistent with our mesoscale observational results and confirm that settling gobies prefer reefs with low rock cover.

When we manipulated rock cover on small habitat patches, there was no evidence that settling gobies distinguished between habitat patches made of beach-rock or reef-rock (ANCOVA: $F_{1,12} = 0.429$, $p = 0.525$; Fig. 5), nor was there an interaction between the effects of rock type and rock cover (ANCOVA: $F_{1,12} = 1.275$, $p = 0.281$; Fig. 5). Most importantly, the percent cover of rocks in a patch exerted no detectable influence on the rate of goby settlement (ANCOVA: $F_{1,12} = 2.069$, $p = 0.176$; Fig. 5). The total number of gobies settling to the habitat patches was relatively small (354) but, like the small-scale observational study, the results of this experiment suggest that settling gobies do not discriminate among small habitat patches based on rock or coral cover.

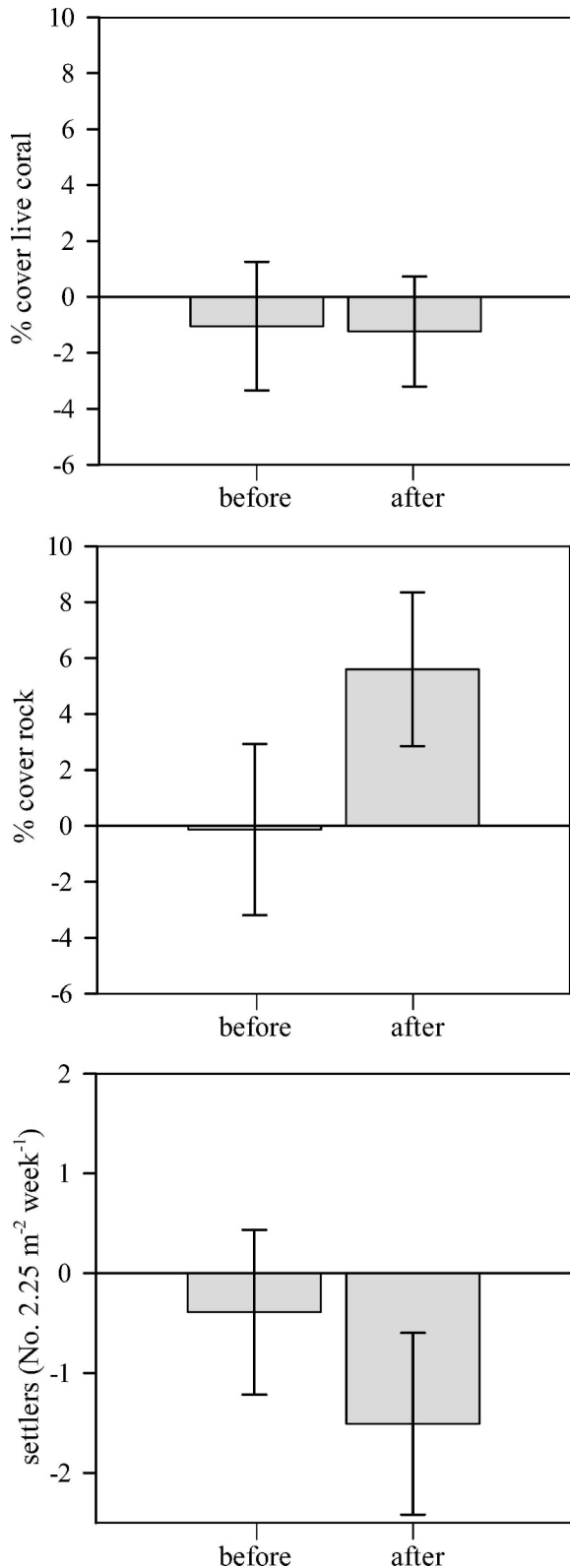


Fig. 4. Response of settling gobies to large-scale rock addition. Plotted are mean differences ($\pm 95\%$ CI) between paired halves of a reef (rock-addition half minus control half). Data from before and after rocks were added are plotted separately.

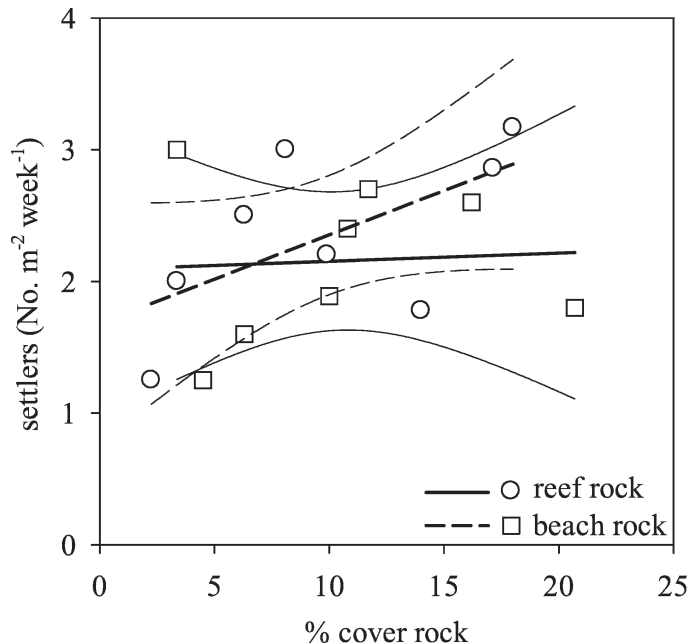


Fig. 5. No response of settling gobies to manipulation of rock cover in small habitat patches. Patches were constructed using rock from local beaches or from nearby reefs. Plotted are the results of a linear regression ($\pm 95\%$ CI) fit separately for each rock-type treatment. Details of statistical analysis are described in the text.

Discussion

Overall, we have shown that the density of newly settled gobies on mesoscale reefs increases as the cover of coral and rock declines, but that no such pattern was evident on microscale patches. We first consider to what extent the density of newly settled gobies reflects the actual larval settlement onto a reef as opposed to some pattern of post-settlement mortality. This question arises because reef-fish larvae can settle each night throughout the summer and then experience some risk of predation during the night of settlement (Planes and Lecaillon 2001) and the following days (Almany and Webster 2006). Because we collected settlers each morning during the small-scale experiment, some settlers may have died during the hours between settlement and collection. In the other components of our study, however, we monitored settlement onto caged plots. We previously showed that caged plots sampled each morning accumulated more settlers than uncaged plots sampled at the same time, which suggests that caging eliminates much of the predation typically experienced by settling larvae during their first night on the reef (Steele and Forrester 2002). We have also demonstrated that weekly collections of settlers from caged plots are comparable to the cumulative catch from collections made every morning (Steele and Forrester 2002), which suggests that predation in the days following settlement is also prevented by caging. These past results, plus the agreement between our two small-scale studies here that employed uncaged and caged plots, suggest that our findings reflect patterns of settlement.

What is the cue that induces larvae to select reefs with low rock and coral cover? Many different cues are possible, because late-stage reef fish larvae have well-developed sensory organs and respond to information from chemical, auditory, visual, and other sources (review by Kingsford et al. 2002). If the gobies are responding to a cue associated with the rock directly, it must be a feature associated with limestone, since this was the material used in the large-scale manipulation. The small-scale experiment eliminated the possibility that the rock's terrestrial origin might have been the source of a cue, because settlers failed to differentiate beach-rock from rock taken from nearby reefs. Another possibility is that the goby larvae are actually responding to some organism, or organisms, whose abundance changed in response to rock cover. Following any manipulation of an intact ecological community, many potential direct and indirect responses can produce similar net effects on any one focal species, making it difficult to pinpoint the ultimate cause of change in goby settlement. However, changes in goby settlement after rock addition occurred within 2 weeks and remained consistent over 3 yr (data not shown). Consequently, if gobies were responding to other organisms, then these organisms must also have responded rapidly and persistently to the rock addition.

Our most puzzling result was that settling gobies appear to respond to rock cover at mesoscales, but not at microscales. This finding suggests that when habitat patches fall below some threshold size, gobies either cannot detect or choose not to respond to the cue(s) that normally stimulate settlement. The coarse-grained nature of the response suggests that this cue might be chemical or auditory. Orientation to both chemical (Sweatman 1988; Atema et al. 2002) and auditory cues associated with reefs (Tolimieri et al. 2004) has been demonstrated over short distances (centimeters to meters). More importantly, some of these cues allow detection of reef properties over larger distances, because larvae can orient to reef sounds at least 80 m distant (Tolimieri et al. 2004) and tidal plumes carrying chemosensory cues can extend a few kilometers downstream from reefs (Atema et al. 2002).

For marine species with pelagic larvae, it is commonly assumed that larvae choose settlement sites that are suitable for post-settlement survival and reproduction (Young 1990). Surprisingly, however, studies clearly linking larval site selection to favorable post-larval conditions are few (Raimondi and Morse 2000). Although all of our study sites lay within the range of coral and rock densities in which adult gobies can persist and reproduce, it is intriguing that settling gobies preferred habitat with low rock and coral cover where adult gobies experience the greatest risk of predation. This habitat-selection pattern may be an example of nonintuitive cue use (Stamps and Krishnan 2005). We suspect that settling gobies might be responding to habitat features important in the first few days after settlement, and that these factors may differ from those important to older juveniles and adults. We know that gobies do not use crevices under hard substrata as refuges in the first few days after settlement, despite the fact that they suffer intense predation during this period. Instead of taking cover, newly settled gobies remain

motionless on the sand when approached and, if attacked, tend to remain on sand in flight. We cannot resolve this puzzle at present, because the ecology of newly settled gobies is little-known.

The main contribution of this study is to provide experimental evidence for active discrimination among mesoscale sites at the time of settlement. Mesoscale correlations between habitat features and juvenile density previously identified by others (Tolimieri 1995; Caselle and Warner 1996; Danilowicz et al. 2001) may perhaps also be due to habitat selection by settling larvae, and need not be explained in terms of larval delivery or post-settlement mortality. Although we did not identify the mechanism by which settling gobies selected among potential settlement sites, the strong swimming ability of late-stage larvae makes active choice among mesoscale sites plausible (Stobutzki and Bellwood 1997). Moreover, there is growing evidence that larval fishes can detect the presence of reefs at distances from hundreds of meters to >1 km (Stobutzki and Bellwood 1998; Leis and Carson-Ewart 2003). The fact that some reef fish larvae can recognize the smell of their natal reef (Gerlach et al. 2007) further supports the possibility of active site-selection at settlement, including the return of larvae to the reef from which they were spawned (Jones et al. 1999). Behavioral choices made by settling larvae may thus set the initial size of benthic populations at larger spatial scales than previously recognized, with potentially important consequences for population and community dynamics.

References

- ALMANY, G. R., AND M. S. WEBSTER. 2006. The predation gauntlet: Early post-settlement mortality in reef fishes. *Coral Reefs* **25**: 19–22.
- ATEMA, J., M. J. KINGSFORD, AND G. GERLACH. 2002. Larval reef fish could use odour for detection, retention and orientation to reefs. *Mar. Ecol. Prog. Ser.* **241**: 151–160.
- BUTMAN, C. A. 1987. Larval settlement of soft-sediment invertebrates—the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. *Oceanogr. Mar. Biol.* **25**: 113–165.
- CALEY, M. J., M. H. CARR, M. A. HIXON, T. P. HUGHES, G. P. JONES, AND B. A. MENGE. 1996. Recruitment and the population dynamics of open marine populations. *Annu. Rev. Ecol. Syst.* **27**: 477–500.
- CASELLE, J. E., AND R. R. WARNER. 1996. Variability in recruitment of coral reef fishes: The importance of habitat at two spatial scales. *Ecology* **77**: 2488–2504.
- DANILOWICZ, B. S., N. TOLIMIERI, AND P. F. SALE. 2001. Meso-scale habitat features affect recruitment of reef fishes in St. Croix, US Virgin Islands. *Bull. Mar. Sci.* **69**: 1223–1232.
- DI BACCO, C., D. SUTTON, AND L. MCCONNICO. 2001. Vertical migration behavior and horizontal distribution of brachyuran larvae in a low-inflow estuary: Implications for bay–ocean exchange. *Mar. Ecol. Prog. Ser.* **217**: 191–206.
- DOHERTY, P. J. 1991. Spatial and temporal patterns of recruitment, p. 261–293. *In* P. F. Sale [ed.], *The ecology of fishes on coral reefs*. Academic Press.
- DOHERTY, P., M. KINGSFORD, D. BOOTH, AND J. CARLETON. 1996. Habitat selection before settlement by *Pomacentrus coelestis*. *Mar. Freshw. Res.* **47**: 391–399.

- FORRESTER, G. E., AND M. A. STEELE. 2004. Predators, prey refuges, and the spatial scaling of density-dependent prey mortality. *Ecology* **85**: 1332–1342.
- GERLACH, G., J. ATEMA, M. J. KINGSFORD, K. P. BLACK, AND V. MILLER-SIMS. 2007. Smelling home can prevent dispersal of reef fish larvae. *Proc. Natl. Acad. Sci. U. S. A.* **104**: 858–863.
- JENKINS, S. R. 2005. Larval habitat selection, not larval supply, determines settlement patterns and adult distribution in two chthamalid barnacles. *J. Anim. Ecol.* **74**: 893–904.
- JONES, G. P., M. J. MILICICH, M. J. EMSLIE, AND C. LUNOW. 1999. Self-recruitment in a coral reef fish population. *Nature* **402**: 802–804.
- KINGSFORD, M. J., J. M. LEIS, A. SHANKS, K. C. LINDEMAN, S. G. MORGAN, AND J. PINEDA. 2002. Sensory environments, larval abilities and local self-recruitment. *Bull. Mar. Sci.* **70**: 309–340.
- KNIGHT-JONES, E. W. 1953. Laboratory experiments on gregariousness during settlement in *Balanus balanoides* and other barnacles. *J. Exp. Biol.* **30**: 584–599.
- LEIS, J. M., AND B. M. CARSON-EWART. 2003. Orientation of pelagic larvae of coral-reef fishes in the ocean. *Mar. Ecol. Prog. Ser.* **252**: 239–253.
- MONTGOMERY, J. C., A. JEFFS, S. D. SIMPSON, M. MEEKAN, AND C. TINDLE. 2006. Sound as an orientation cue for the pelagic larvae of reef fishes and decapod crustaceans. *Adv. Mar. Biol.* **51**: 143–196.
- PARIS, C. B., AND R. K. COWEN. 2004. Direct evidence of a biophysical retention mechanism for coral reef fish larvae. *Limnol. Oceanogr.* **49**: 1964–1979.
- PINEDA, J. 1991. Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. *Science* **253**: 548–551.
- PLANES, S., AND G. LECAILLON. 2001. Caging experiment to examine mortality during metamorphosis of coral reef fish larvae. *Coral Reefs* **20**: 211–218.
- RAIMONDI, P. T., AND A. N. C. MORSE. 2000. The consequences of complex larval behavior in a coral. *Ecology* **81**: 3193–3211.
- SALE, P. F., W. A. DOUGLAS, AND P. J. DOHERTY. 1984. Choice of microhabitats by coral-reef fishes at settlement. *Coral Reefs* **3**: 91–99.
- SHANKS, A. L. 1995. Mechanisms of cross-shelf dispersal of larval invertebrates and fish, p. 323–368. *In* I. McEdward [ed.], *Ecology of marine invertebrate larvae*. CRC Press.
- , AND W. G. WRIGHT. 1987. Internal-wave-mediated shoreward transport of cyprids, megalopae, and gammarids and correlated longshore differences in the settling rate of intertidal barnacles. *J. Exp. Mar. Biol. Ecol.* **114**: 1–13.
- SPONAUGLE, S., AND R. K. COWEN. 1994. Larval durations and recruitment patterns of two Caribbean gobies (Gobiidae): Contrasting early life histories in demersal spawners. *Mar. Biol.* **120**: 133–143.
- STAMPS, J., AND V. V. KRISHNAN. 2005. Nonintuitive cue use in habitat selection. *Ecology* **86**: 2860–2867.
- STEELE, M. A., AND G. E. FORRESTER. 2002. Early postsettlement predation on three reef fishes: Effects on spatial patterns of recruitment. *Ecology* **83**: 1076–1091.
- STOBUTZKI, I. C., AND D. R. BELLWOOD. 1997. Sustained swimming abilities of the late pelagic stages of coral reef fishes. *Mar. Ecol. Prog. Ser.* **149**: 35–41.
- , AND ———. 1998. Nocturnal orientation to reefs by late pelagic stage coral reef fishes. *Coral Reefs* **17**: 103–110.
- SWEATMAN, H. P. A. 1988. Field evidence that settling coral-reef fish larvae detect resident fishes using dissolved chemical cues. *J. Exp. Mar. Biol. Ecol.* **124**: 163–174.
- THORROLD, S. R., J. M. SHENKER, R. MOJICA, E. D. MADDOX, AND E. WISHINSKI. 1994. Temporal patterns in the larval supply of summer-recruiting reef fishes to Lee-Stocking Island, Bahamas. *Mar. Ecol. Prog. Ser.* **112**: 75–86.
- TOLIMIERI, N. 1995. Effects of microhabitat characteristics on the settlement and recruitment of a coral reef fish at two spatial scales. *Oecologia* **102**: 52–63.
- , O. HAINE, A. JEFFS, R. MCCAULEY, AND J. MONTGOMERY. 2004. Directional orientation of pomacentrid larvae to ambient reef sound. *Coral Reefs* **23**: 184–191.
- YOUNG, C. M. 1990. Larval ecology of marine-invertebrates—a sesquicentennial history. *Ophelia* **32**: 1–48.
- , AND F. S. CHIA. 1987. Abundance and distribution of pelagic larvae as influenced by predation, behavior, and hydrographic factors, p. 385–463. *In* A. C. Giese, J. S. Pearse and V. B. Pearse [eds.], *Reproduction of marine invertebrates*. Blackwell Scientific.

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