

Jacqueline Wilson · Craig W. Osenberg

## Experimental and observational patterns of density-dependent settlement and survival in the marine fish *Gobiosoma*

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**Abstract** Dynamics of reef fishes are influenced by settlement and post-settlement processes. How these processes co-vary or interact is often overlooked due to a focus on one process or study design. We approached this problem by conducting both observational and experimental studies of settlement and post-settlement survival in two goby species, *Gobiosoma evelynae* and *G. prochilos*, in Tague Bay of St. Croix, U.S. Virgin Islands. Settlement to coral heads on patch reefs was spatially variable, but the spatial patterns were relatively consistent through time: certain coral heads repeatedly received many settlers, while others received few. We investigated factors that could influence settlement and therefore contribute to the patchy distribution of settlers. Coral heads that received more settlers were larger and further from the center of the reef than heads with few settlers. The heads with many settlers also had more resident fishes, suggesting that resident fishes might attract settlers. We conducted a large-scale fish removal experiment and found that variation in settlement rates to coral heads was mostly driven by inherent properties of the coral heads and not by the presence of resident fishes. We then conducted a replicated, smaller-scale experiment, which showed that increasing density of resident fishes decreased settlement and post-settlement survival. Observational data, however, showed that settlers survived at comparable rates on coral heads with high and low fish density. We discuss several alternative hypotheses that might explain this discrepancy in the strength of density-dependence between the observational and experimental studies. One of these explanations, which has not been considered in the literature, is that the difference in the results arose through a correlation between settlement intensity and the quality of either the larvae or the site to which they settled. As a result, higher settlement may not necessarily lead to higher mortality. We

develop a graphical model that shows how density-dependence and habitat or larvae quality may interact. Such a model may help to resolve some of the contradictory results obtained among studies of reef fishes.

**Keywords** Density-dependence · Settlement · Post-settlement survivorship · Competition · Reef fishes

### Introduction

Many marine organisms, such as reef fishes, are characterized by a complex life cycle consisting of a dispersive, pelagic larval stage followed by a relatively site-attached, adult phase (Sale 1980; Thresher 1984; McEdward 1995). Spatial and temporal variation in larval settlement can have strong effects on the distribution, size and age structure, and dynamics of these open populations (Victor 1983; Gaines and Roughgarden 1985; Doherty 1991; Carr 1994). Processes that occur after settlement (e.g., mortality due to predation) can modify these initial settlement patterns (Steele 1997; Forrester and Steele 2000). Consequently, understanding the factors that contribute to variation in settlement and post-settlement survival is critical to understanding spatial and temporal variation in the abundance of reef organisms (Levin 1993; Olafsson et al. 1994).

Variability in the distribution and abundance of reef fishes has been explained using two arguments that differ in their assumptions regarding the relative importance of settlement versus post-settlement processes. In its extreme, the settlement limitation hypothesis argues that an increase in settlement will lead to a proportional increase in recruitment because reefs are under-saturated, and post-settlement mortality is density-independent (Doherty 1981, 1991; Doherty and Williams 1988). As a result, variation in benthic population dynamics can be explained solely by studying spatial and temporal variation in settlement. In contrast, proponents of post-settlement processes argue that density-dependent mortality is sufficiently strong to reshape any initial patterns established

J. Wilson (✉) · C.W. Osenberg  
Department of Zoology, University of Florida, Gainesville,  
FL 32611–8525, USA  
e-mail: jwilson@zoo.ufl.edu  
Fax: +1-352-3923704

by variation in settlement (Behrens 1987; Jones 1987; Caley 1995; Forrester 1995). Unlike settlement, the strength of density-dependence is often assumed to be homogeneous in space and time (e.g., Schmitt et al. 1999).

There are several problems with these divergent approaches. First, larval supply (and settlement) and density-dependence can simultaneously affect local abundance and population structure – they do not act in isolation (Warner and Hughes 1988; Chesson 1998; Hixon 1998; Schmitt et al. 1999). Second, settlement itself can be density-dependent (Sweatman 1983, 1985; Schmitt and Holbrook 1996). Thus, density-dependence cannot only reshape settlement patterns (via subsequent mortality), but it can also directly influence these initial patterns. Third, the strength of density-dependence may vary spatially (and temporally) and thus contribute to patterns falsely interpreted as driven by variation in larval supply. Fourth, the strength of factors that influence settlement and the factors that influence density-dependence may be correlated in space (or time), and this covariation can give rise to different results in observational versus experimental studies. Interestingly, in an ongoing meta-analysis of density-dependence in reef fishes, only 12% of published studies of density-dependent survival report both experimental and observational results (Osenberg et al., unpublished data). Although experimental studies can eliminate confounding influences, observational studies can reveal new insights about systems if the observed patterns fail to mirror experimental results (and thus indicate the correlated effects of other variables). As a result, it is critical that there be more studies that simultaneously address both settlement and post-settlement processes in both an experimental and observational setting. We take this integrated approach in our studies of two species of cleaning gobies, *Gobiosoma evelynae* and *G. prochilos*.

## Materials and methods

### Study site and species

We conducted our work in Tague Bay on the northeast part of St. Croix (17°45'40"N, 65°35'30"W) in the U.S. Virgin Islands during the summers of 1995 and 1996. We conducted surveys and experiments in the eastern part of the bay on three patch reefs (nos. 5, 7, 18 – as in Gladfelter et al. 1980) during 1995 and 1996 and on the backreef (the bay side of the barrier reef near the patch reefs) during 1996.

The study organisms, *G. evelynae* and *G. prochilos*, are small (<34 mm standard length, SL) cleaning gobies in the subgenus *Elacatinus* that can remove ectoparasites from larger fishes (Colin 1975). In Tague Bay, however, we rarely observed cleaning behavior. Instead, the fishes fed primarily on zooplankton. These two species are relatively sedentary, dwell on live scleractinian corals (and occasionally on rock surfaces and the outer surface of sponges), and occur at depths from zero to 50 m. The two species are very similar ecologically and typically occupy the same coral heads in areas where their distributions overlap (the central Caribbean). The species are also morphologically similar but can be distinguished by subtle differences in their color patterns and jaw morphology. They mature at around 20–25 mm SL, with an expected maximum life expectancy of approximately 1 year (Colin 1975).

### Natural patterns

#### Settlement

During the summers of 1995 (June and July) and 1996 (May–July), we conducted bi-weekly surveys on the three patch reefs to quantify spatial and temporal variation in the settlement patterns of these two fish species. Settlement occurs on a lunar cycle, with settlement beginning as early as the third quarter moon, peaking around the new moon, and continuing as late as the first quarter moon (a period as long as 2 weeks, but typically much less). New settlers lack pigmentation for approximately 24 h after settling on coral heads, allowing settlers to be easily distinguished from older fishes. Typically, settlement is defined as the number of larval fish that leave the pelagic environment and settle to a demersal habitat, and recruitment is the number of fish that survive some arbitrary amount of time after settlement (see Keough and Downes 1982 for discussion on the terms settlement and recruitment). Although at most times our surveys provided very close estimates of true settlement (surveys were done the morning after a settlement pulse), some mortality had likely occurred before the surveys were conducted. However, in order to avoid confusion, we use the term “settler” (and settlement) for fishes that arrived during one settlement event. We use the term “recruit” (and recruitment) for fishes that survived to the next settlement event.

During two settlement events in 1995 (24 June–2 July and 30 July) and three settlement events in 1996 (13–17 May, 17–19 June and 15–16 July), we thoroughly searched all coral heads on each patch reef ( $n=224$ ) and recorded the number and age-class of gobies on each coral head: “settlers” (<2 weeks post-settlement; typically <3 days and <13 mm), “recruits” (2–4 weeks post-settlement; approximately 20–25 mm), and “adults” ( $\geq 4$  weeks or >25 mm). These coral heads were individually numbered for subsequent characterization (see below). In 1996, but not 1995, we were able to distinguish between the two goby species in the field. We verified the field identifications by re-identifying the fishes under a dissecting microscope according to Colin (1975). The 1996 data showed similar patterns of settlement for the two species. Because these species are ecologically similar and sometimes hybridize (Colin 1975), we combined data from the two species and report data from both 1995 and 1996.

#### Physical characteristics of coral heads

In 1995 we mapped each reef, recording the location and species of each coral head. We also measured all coral heads for the ten coral species upon which we observed at least one goby during the course of the study: *Siderastrea siderea*, *S. radiana*, *Stephanocoenia michilini*, *Montastrea annularis*, *M. cavernosa*, *Porites asteriodes*, *Diploria strigosa*, *D. clivosa*, *D. labyrinthiformis*, and *Millepora* spp. We measured each coral head's surface area by placing a grid over the surface of the coral and calculating the area covered by live coral. We also measured each coral head's height and elevation (i.e., the vertical distance from the base of a patch reef to the top of the coral head). In addition, we measured the shortest distance from the center of each head to the edge of the reef. Coral heads connected to the main portion of the patch reef were assigned negative distances whereas those just off the main part of the patch reef were assigned positive distances.

#### Data analyses

There is no single best way to quantify fish density (e.g., per head, unit area, or unit volume). Other work has shown that fish density (measured on per unit area), and fish number (per coral head), independent of density, can both have significant effects on fish dynamics (Shima 2001). We analyzed the data on a per coral head and per unit area. Both measures of density gave similar results for most analyses. Because coral heads are the most natural unit of measurement, we presented results for the number of fishes per

coral head. When interpretations were sensitive to the measurement of density, we presented both sets of analyses.

Average density can greatly underestimate the density actually experienced by an individual (Folt and Schulze 1993; Folt et al. 1993). Therefore, we used Lloyd's Mean Crowding Index (Lloyd 1967),  $m$ , which in our system estimates the average number of other fishes that shared a coral head with a focal fish:

$$m = \sum_{i=1}^N X_i / N \quad (1)$$

where  $N$ =the total number of settlers sampled across all coral heads, and  $X_i$ =the number of other settlers that shared the coral head with the  $i$ th fish. We estimated  $m$  for settlers experiencing other settlers, and we also modified the index to estimate the average number of older fishes experienced by settlers. In this latter case,  $X_i$  corresponded to the number of older fishes, rather than the number of other settlers, that shared a coral head with a settler.

To characterize the temporal consistency of the spatial patterns, we correlated the number of settlers on a coral head for each pair of surveys. We also summarized the inter-annual consistency of settlement. In these analyses, we excluded coral heads that never received a settler during the five settlement events [which made the test more conservative by eliminating a large number of (0, 0) observations] and also excluded coral heads that were manipulated as part of the patch reef experiment in 1995 (see below). The numbers of settlers were square root transformed to homogenize variances (Sokal and Rohlf 1995).

To investigate the influence of older fishes on settlement, we examined the correlation between settlement and the number of fishes present on a coral head within 2 weeks before each settlement event [we used a sequential Bonferroni test to adjust  $P$ -values for the multiple correlations (Holm 1979)].

To examine the relationship between coral physical attributes and settlement, coral heads were separated into five categories based on the average number of settlers received for the three settlement events in 1996: (1) "lowest": no settlers in 1996; (2) "lower": 0–1 settlers/event; (3) "moderate": 1–2 settlers/event; (4) "higher": 2–4 settlers/event; and (5) "highest":  $\geq 4$  settlers/event. This part of the study was limited to 1996 to avoid the possible confounding effects associated with the 1995 experiment. One-way ANOVAs were performed to determine if coral surface area, height, elevation, distance from the edge of patch reef, and fish density varied among the different settlement categories. Surface area and height were log transformed and density was square root transformed to homogenize variances (Sokal and Rohlf 1995).

We also estimated survivorship among the different settlement categories following three settlement events (June–July 1995, May–June 1996 and June–July 1996). Young fish do not move among coral heads, and the size-distributions of the most recent cohort remained distinct from previous cohorts (Wilson, personal observation). Therefore, we calculated monthly survivorship as the ratio of the number of juveniles alive approximately 1 month after the settlement pulse to the number of fishes first recorded after the settlement pulse. Survival was arcsine square root transformed to help normalize distributions and homogenize the variances (Sokal and Rohlf 1995).

#### *Field experiment: facilitation by conspecifics versus the effect of coral attributes*

Some coral heads consistently received high levels of settlement and had high densities of resident gobies. To distinguish between a facilitative effect of older fishes from an effect of the physical and/or biological attributes of the coral heads unrelated to fish presence, we performed a large-scale fish removal on the patch reefs in 1995. Before settlement in June 1995, we surveyed all gobies on the three patch reefs. We then removed all the gobies from coral heads on reef 5 and from coral heads on one half of reef 18. Fishes on reef 7 and on the other half of reef 18 were left as controls. Surveys were conducted each morning during the June

settlement pulse (24 June–2 July 1995). Settlers were removed daily, and the total number of settlers to each head was summed over the settlement event. If physical and biological properties of the coral heads primarily influenced settlement, then the previously observed pattern of settlement should persist even after the removal of resident gobies. In contrast, if larvae settle preferentially to coral heads with resident fishes, then the removal of residents should obscure the observed spatial variation in settlement. We used analysis of covariance to test if the presence (or absence) of residents affected settlement. The number of older residents present on coral heads before the June settlement event was the covariate, and residents present or removed was the treatment. Settlement was square root transformed (Sokal and Rohlf 1995).

#### *Field experiment: density-dependence and age-class effects*

To examine the effect of density and age-structure on settlement and survival, we conducted a second experiment separated into two phases using a more homogeneous set of coral heads. This necessitated conducting the experiment on the backreef immediately adjacent to the patch reefs, which contained more coral heads of the most preferred coral species (see below). Goby distribution (abundance and spatial variation) in the backreef area was similar to that of the adjacent patch reefs (Wilson 1998). Approximately 90% of *G. evelynae* and *G. prochilos* in the backreef area were found on *Montastrea annularis*, and *M. annularis* was the most abundant coral species in the backreef area. For the experiment, we therefore selected 30 *M. annularis* coral heads that had similar numbers of resident gobies and were similar in surface area, height and elevation.

We established a target-neighbor experiment (Goldberg and Werner 1983; Olson et al. 1995) with five treatments by removing all resident gobies and adding different numbers of older individuals ( $\geq 20$  mm or older than 1 month, which we call adults) and settlers ( $< 13$  mm or individuals younger than 2 weeks) to these coral heads. Four treatments formed a cross-classified design with neighbor age-class (adults or settlers) crossed with neighbor density (low or high). Low density was two adults or four settlers; high density was four adults or eight settlers and was based on the average 1996 crowding observed at these sites. The fifth treatment had zero neighbors. Treatments were set-up and maintained with a random mixture of the two species of gobies based on the natural distribution of these fishes in the study area. The 30 coral heads were originally separated into six blocks with one replicate per treatment per block. Preliminary analysis, however, showed the main effect of blocks was not significant ( $P=0.61$ ), so the blocking term was subsequently dropped from the analyses.

The first phase of the experiment was designed to quantify the effect of previously settled fishes on subsequent settlement. During one settlement pulse (8–15 June 1996) experimental heads were surveyed daily. New settlers were counted and removed each day so that effects of new settlers would not be confounded with effects of neighbors. Missing neighbors were replaced to maintain treatments.

The second phase of the experiment (23 June–12 July 1996) was designed to measure the post-settlement survival of target settlers under the same density regimes on the 30 coral heads. Treatments were re-established according to the same experimental design above, except that three target settlers (9 mm SL, *G. evelynae*) were added to each head. The heads were surveyed every 3 days for a total of 12 days and the number of surviving targets and neighbors were recorded. Missing neighbors were recorded and replaced every 3 days to maintain treatments, but target fish were not replaced. Periodic surveys of the study site showed that tagged fish were not appearing on new coral heads, so the disappearance of a target individual was assumed to be due to mortality.

To distinguish the target settlers from other fishes, target fish were tagged subcutaneously with Visible Implant Fluorescent Elastomer (Northwest Marine Technology 1995). A previous tagging experiment showed that handling-related mortality was restricted to the first 2 days after tagging (Wilson 1998). Therefore,

tagged fish were kept in the laboratory for 2 days before being placed on the experimental coral heads.

For the first phase of the experiment, we based the analysis on the cumulative number of settlers over the 8-day period. Using data from the second phase of the experiment, we quantified the average longevity, or average number of days a target remained alive, for each coral head. Because surveys were done every 3 days, we assumed that when a fish disappeared that it had died 1.5 days after its last sighting. Fishes that were still alive after 12 days were assumed to have died 1.5 days later (which made the test more conservative). Because neighbors were monitored daily during the first phase of the experiment, we also estimated the average daily survival of neighbors (settlers and adults) by calculating the fraction of neighbors that had survived from the previous day and averaging this proportion across the 8 days of the experiment. Settlement and longevity were square root transformed; neighbor survivorship was arcsine square root transformed (Sokal and Rohlf 1995).

One-way ANOVAs with orthogonal contrasts were used to analyze the experimental data. For both phases orthogonal contrasts consisted of "absence versus presence" of neighbors, "adults versus settlers", "low versus high density" and an interaction term between age-class and density. A similar design was used to analyze the daily survival of neighbors, except that there were no data available for the "zero neighbor" treatment.

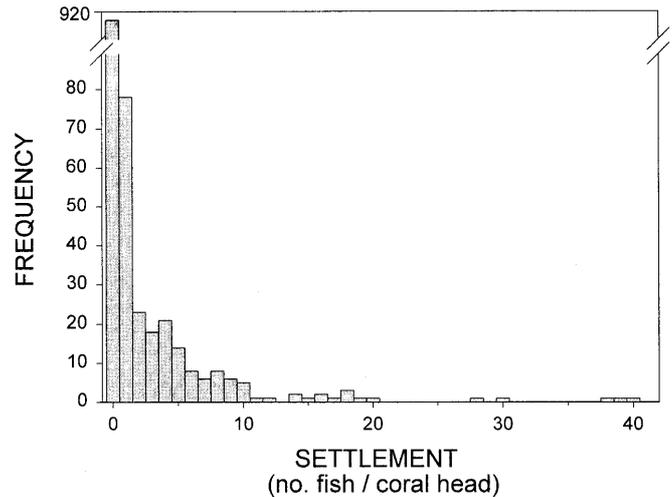
## Results

### Natural patterns

Settlers on the patch reefs were clumped in their distribution with most of the coral heads having no or few settlers and a few coral heads having most of the settlers (Fig. 1). The average settler experienced 3.7 adults and 9.6 settlers on its coral head. There was, however, considerable variation in crowding over the five settlement events, ranging from 2.4 to 6.2 adults and from 1.1 to 22.2 settlers.

Coral heads that had many settlers at one event tended to receive many settlers during subsequent events. There were statistically significant correlations between the numbers of settlers during all pairs of settlement events except for the first two (Table 1 a). This pattern held up within years (Table 1 a), as well as between years; coral heads with many settlers in 1995 had many settlers in 1996 ( $r^2=0.67$ ,  $P<0.0001$ ,  $n=39$ ).

**Table 1** Spatial and temporal variation in settlement. Spatial correlation between settlement in each of five time periods, and correlation between settlement and the number of resident fishes present during the same five time periods. Only coral heads that had settlers on them during at least one settlement event were in-



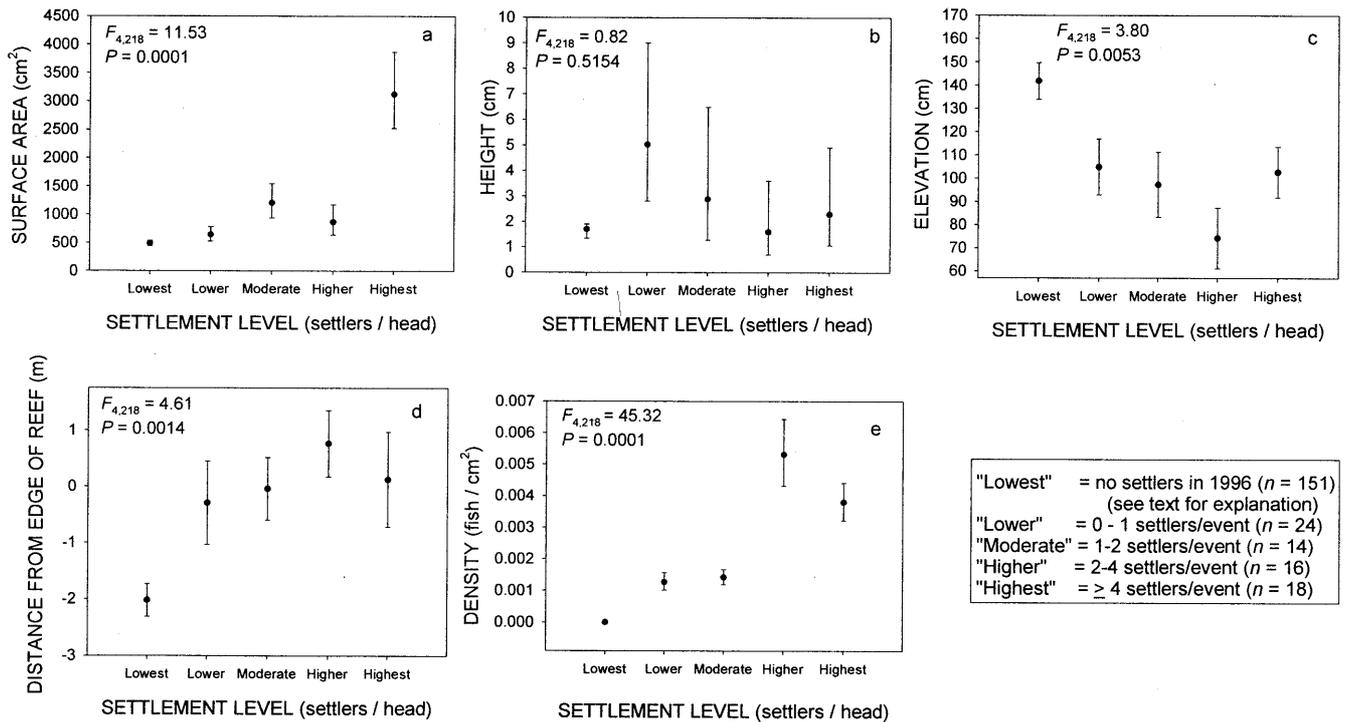
**Fig. 1** Frequency distribution of the number of settlers on coral heads from three patch reefs for the five settlement events during 1995 and 1996. Coral heads that were manipulated during the 1995 patch reef experiment were not included in the frequency distribution

Settlement to a coral head was significantly correlated with the density of older fishes present just before the settlement event (Table 1 b). The coral heads that received the greatest number of settlers also tended to be larger (greater surface area) (Fig. 2a), closer to the base of the patch reefs (lower elevation: Fig. 2c) and on the edge or off the patch reef (more positive distances: Fig. 2d). However, there was no statistically significant difference in height of coral heads among the different settlement-level categories (Fig. 2b). Despite their larger area, the coral heads that received more settlers also had a greater areal density of settlers (Fig. 2e).

Despite the wide range in settlement intensity, there was no consistent pattern in the survival of settlers (Fig. 3). A repeated measures ANOVA on the transformed data showed no statistically significant differences in survival among the different settlement intensities or different time periods (effect of settlement intensity:  $F_{3,34}=1.00$ ,  $P=0.40$ ; effect of time:  $F_{2,34}=0.64$ ,

cluded. Heads that were manipulated in June 1995 were excluded in the correlation analyses involving the 24 June – 2 July 1995 event. Data were square root transformed. Below each correlation coefficient is the associated  $P$ -value and sample size ( $n$ , the number of coral heads)

	Settlement event			
	30 July 1995	13–17 May 1996	17–19 June 1996	15–16 July 1996
Between settlement events				
24 June–2 July 1995	0.265, $P=0.1033$ , $n=39$	0.632, $P<0.0001$ , $n=39$	0.609, $P<0.0001$ , $n=39$	0.611, $P<0.0001$ , $n=39$
30 July 1995	–	0.294, $P=0.008$ , $n=80$	0.369, $P=0.0007$ , $n=80$	0.366, $P=0.0008$ , $n=80$
13–17 May 1996	–	–	0.579, $P<0.0001$ , $n=80$	0.543, $P<0.0001$ , $n=80$
17–19 June 1996	–	–	–	0.551, $P<0.0001$ , $n=80$
Between settlement and residents				
24 June–2 July 1995	30 July 1995	13–17 May 1996	17–19 June 1996	15–16 July 1996
0.710, $P<0.0001$ , $n=39$	0.322, $P=0.0036$ , $n=80$	0.756, $P<0.0001$ , $n=80$	0.674, $P<0.0001$ , $n=80$	0.542, $P<0.0001$ , $n=80$



**Fig. 2a–e** Physical attributes of coral heads on the patch reefs as a function of settlement level (based on mean settlement in 1996). **a** Surface area, **b** height of the coral head, **c** elevation (vertical distance from the base of the patch reef to the top of the coral head), **d** horizontal distance from the edge of the patch reef to the center of the coral head (negative values indicate the distance onto the patch reef; positive values indicate the distance away from the patch reef), and **e** overall density of settlers. ANOVAs for surface area measurements (**a**) and height measurements (**b**) were performed on log transformed data, and ANOVA for density measurements were performed on square root transformed data. Back-transformed means and standard errors are shown. Sample size ( $n$ ) refers to the number of coral heads in each settlement category

$P=0.56$ ), although there was a significant effect of coral head nested within settlement intensity ( $F_{60,34}=2.03$ ,  $P=0.014$ ) and a significant interaction effect between settlement intensity and time ( $F_{5,34}=4.12$ ,  $P=0.005$ ). This interaction term makes interpretation of the main effects (e.g., settlement intensity) problematic; however, time was a random effect and the effect of settlement showed no consistent pattern of variation through time. Indeed, based on separate ANOVAs there were no statistically significant effects of settlement intensity for any of the periods (Fig. 3a–c), or for survivorship averaged across the three time periods (Fig. 3d;  $F_{3,64}=1.69$ ,  $P=0.16$ ). Even though there were large differences in initial density, settlers survived at approximately equal rates across all categories ( $0.270 \pm 0.057$ ; Fig. 3d).

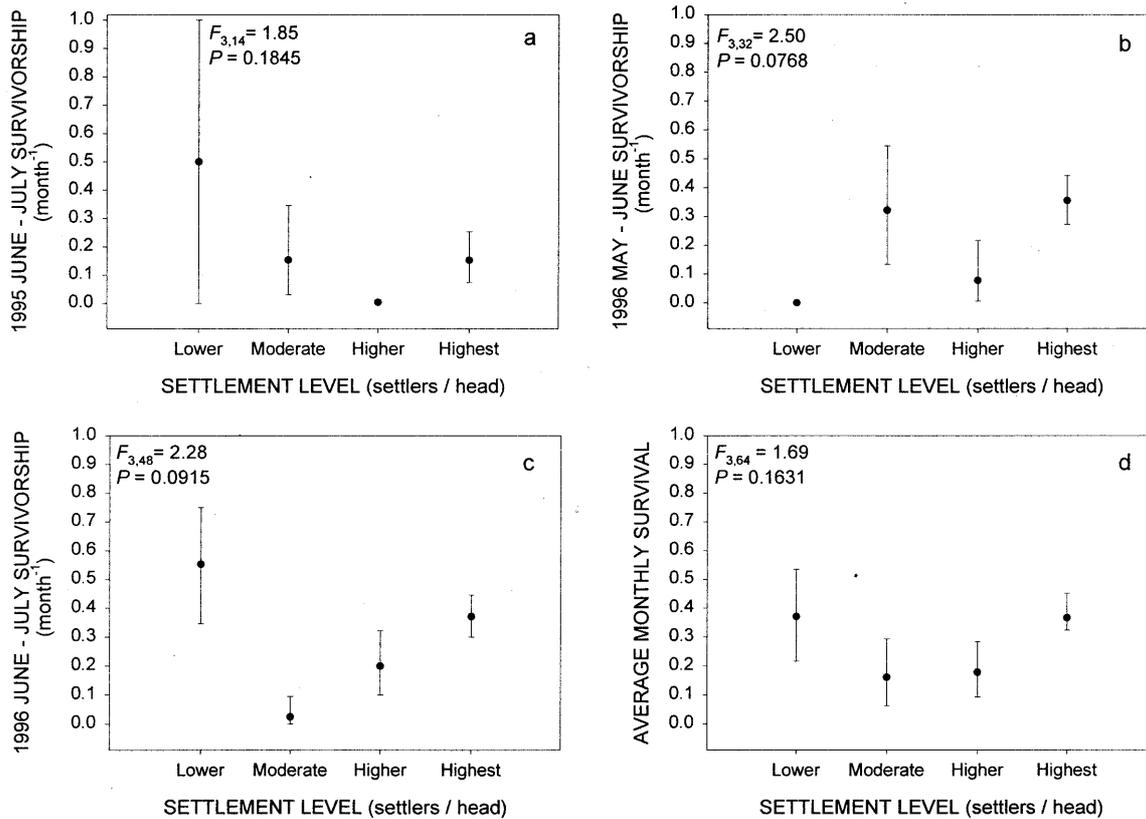
These results were slightly different if density was expressed per unit area. As above, there was no significant effect of settlement intensity ( $F_{3,49}=1.34$ ,  $P=0.27$ ) or time ( $F_{2,49}=0.35$ ,  $P=0.72$ ) on survivorship; unlike the first analysis, however, there was no significant effect of coral heads nested within settlement intensity ( $F_{55,49}=0.78$ ,  $P=0.82$ ) or a significant interaction between settle-

ment intensity and time ( $F_{6,49}=0.24$ ,  $P=0.96$ ). Survivorship averaged across the three time periods did not differ significantly ( $0.30 \pm 0.06$ ;  $F_{3,59}=0.87$ ,  $P=0.49$ ).

#### Field experiments: effects of density and age-structure

For the June 1995 settlement event, there was a statistically significant correlation between settlement and the number of resident fishes, even after these residents had been removed ( $r=0.67$ ,  $n=55$ ,  $P<0.0001$ ). There was also a strong correlation for the control coral heads, where residents were not removed ( $r=0.77$ ,  $n=50$ ,  $P<0.0001$ ). These two relationships were not statistically distinguishable (ANCOVA: resident presence/absence:  $F_{1,101}=0.00$ ,  $P=0.98$ ; interaction between resident density and presence/absence:  $F_{1,101}=1.76$ ,  $P=0.08$ ). These results suggest that characteristics of the coral heads and not the resident fishes were primarily responsible for the observed variation in settlement (e.g., Fig. 1). However, this experiment is pseudoreplicated at the scale of patch reefs, and these inferences should be drawn cautiously; this limitation was overcome in the following experiment.

In our second field experiment, settlement was negatively density-dependent with greater settlement on coral heads with low densities than high densities of neighbors (one-way ANOVA with treatment as main effect;  $F_{4,25}=2.79$ ,  $P=0.048$ ) (Fig. 4a). Orthogonal contrasts revealed no statistically significant differences in settlement between coral heads lacking neighbors and those with neighbors present ( $F_{1,25}=0.65$ ,  $P=0.43$ ), but the contrast of low versus high neighbor density was significant ( $F_{1,25}=5.81$ ,  $P=0.024$ ), with settlement lowered by 30–70% at high neighbor densities. There was a margin-



**Fig. 3a-d** Monthly survival of gobies (for three different time periods) as a function of settlement level (based on the mean settlement in 1996). **a** June–July 1995, **b** May–June 1996, **c** June–July 1996 and **d** the average survival for all three time periods. ANOVA was performed on arcsine square root transformed estimates of survival. Back-transformed means and standard errors are shown. Mean survival for the different time periods was determined from sample sizes that ranged from 5 coral heads per settlement category to 26 coral heads per settlement category

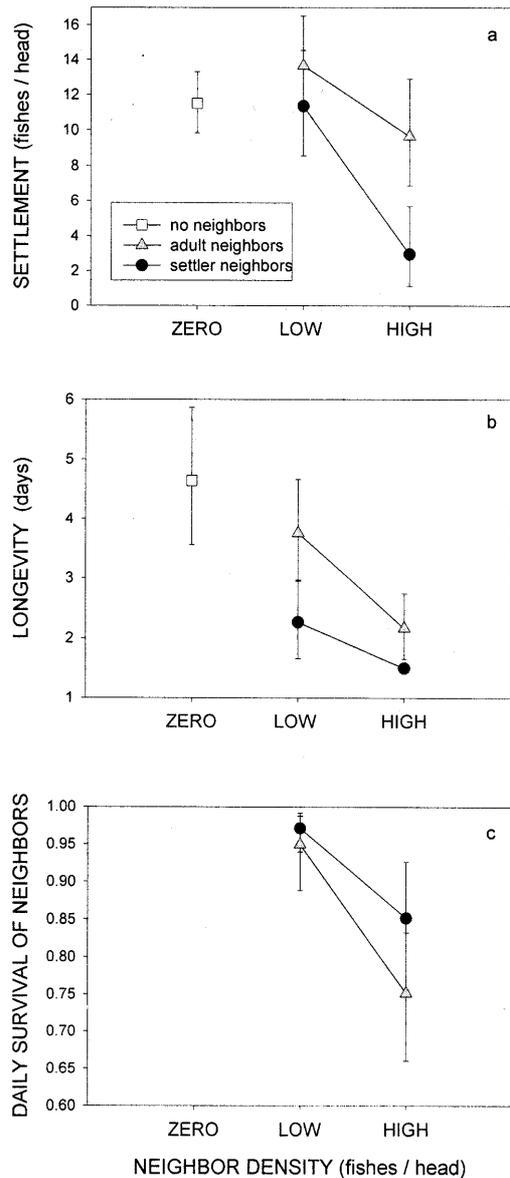
ally significant effect of age-class of neighbors with higher settlement on treatments with adults present than treatments with settlers present ( $F_{1,25}=3.41$ ,  $P=0.077$ ), but there was no significant interaction between age-class and density ( $F_{1,25}=1.31$ ,  $P=0.26$ ).

Post-settlement survivorship was low for all treatments, with approximately 50% of fishes dying even in the low-density treatments. Fewer than 20% of all fishes were alive after 12 days. Such high mortality has also been reported in other studies (Carr and Hixon 1995; Caselle 1999). Longevity (the number of days a fish remained alive after the start of the experiment) from day 0 to day 12 declined with increasing adult and settler density (Fig. 4b; one-way ANOVA with treatment as main effect;  $F_{4,25}=3.53$ ,  $P=0.021$ ) and was greater in the absence of neighbors than in their presence (orthogonal contrast:  $F_{1,25}=7.59$ ,  $P=0.011$ ). Orthogonal contrasts also revealed marginally statistically significant effects of neighbor age-class and density on longevity ( $F_{1,25}=2.85$ ,  $P=0.10$ ;  $F_{1,25}=3.25$ ,  $P=0.075$ ), where adults had a smaller effect on longevity than settlers. There

was no significant interaction between age-class and density ( $F_{1,25}=0.22$ ,  $P=0.65$ ). The effect of density on survival was primarily due to effects that arose between day 0 and day 3. For example, longevity measured after day 3 was not significantly different among treatments (overall effect:  $F_{3,10}=0.27$ ,  $P=0.85$ ), although it was correlated with longevity measured from day 0 ( $r=0.80$ ,  $n=14$ ,  $P=0.0006$ ). However, because survivorship was low, the total sample size was reduced by >50% in analyses that exclude the first 3 days. There were no fish alive (and therefore no estimates of longevity) in the high-density treatments. As a result, the analyses lacked power.

Like tagged settlers, untagged neighbors also survived better at low density than high density (Fig. 4c:  $F_{1,20}=6.21$ ,  $P=0.022$ ). There was no significant difference in survival of different age-classes nor was there a significant interaction between age-class and density ( $F_{1,20}=0.77$ ,  $P=0.39$ ;  $F_{1,20}=0.11$ ,  $P=0.74$ ).

Although we selected coral heads with a similar number of resident gobies, surface area, height, and elevation, there were still differences that might have influenced patterns of settlement and post-settlement survival. Thus, we did a series of ANCOVAs for the settlement and post-settlement survivorship data with the original number of resident gobies, surface area, height, and elevation of coral head as covariates. There were no statistically significant effects of these covariates on any of the experimental data, so we ruled out any additional role of these coral head attributes on the experimental results.



**Fig. 4a-c** Effects of density and age-class on the settlement and survival of fishes from the field experiment. Back-transformed means and standard errors ( $n=6$ ) are shown in each panel. **a** Cumulative level of settlement over 8 days (8–15 June 1996) to coral heads that differed in the density and age-class of neighbors. Cumulative settlement was square root transformed. **b** Longevity (the average number of days a target settler remained alive) of the three target settlers on the different treatments. Longevity was square root transformed. **c** Daily survivorship of neighbors (i.e., the fraction of neighbors that had survived from the previous day) during 8 days (8–15 June 1996). Daily survivorship was arcsine square root transformed

## Discussion

In this study, settlement was variable among coral heads and resulted in a patchy distribution of fishes. Previous studies of marine organisms have attributed spatial variation in settlement to an assortment of different mechanisms, including large-scale circulation patterns

(Roughgarden et al. 1988; Farrell et al. 1991; Gaines and Bertness 1992), small-scale hydrodynamics (e.g., Butman 1987), depletion of larvae from a water mass as it passes over successive settlement sites (Cowen 1985; Gaines et al. 1985), and responses of larvae to settlement cues (Morse and Morse 1984; Shepherd and Turner 1985; Pennings 1993). Settlement cues could include chemicals associated with the substrate (e.g., Morse and Morse 1984) or conspecifics (Raimondi 1988). Our experiments suggested that cues from conspecifics did not facilitate settlement, although this has been observed in other coral reef fishes (Sweatman 1983, 1985; Booth 1992; Schmitt and Holbrook 1996). Instead, conspecifics may actually reduce settlement (Fig. 4a) and thus reduce spatial variation in fish density. Other features of coral heads (e.g., their location; Fig. 2d) may explain the patchy settlement, and although our studies were insufficient to implicate a specific mechanism, they suggested that the mechanism must involve a persistent feature of the coral head to account for the temporal consistency in the settlement patterns (e.g., Table 1). Although our observational data showed that settlement was naturally greater to coral heads with a greater number of residents, our experiments showed that residents had a negative, not positive, effect on settlement. Thus, in the absence of this density-dependence, settlement would have been even more variable.

The implications of the variable settlement are potentially profound, depending on the strength of post-settlement density-dependence. Our observational and experimental studies found conflicting patterns in density-dependent survival: the surveys failed to detect an effect of density on survival (Fig. 3), whereas the experiment demonstrated strong negative effects (Fig. 4b). There are several plausible explanations for this discrepancy.

One possibility is that the two studies shared the same intensity of density-dependence but that our power to detect density-dependence in the observational study was lower. Because the fit of a non-linear Beverton-Holt recruitment function to our recruitment data (Fig. 5a) was not a significant improvement over the linear fit ( $r^2=0.75$  for both), we assumed that density-dependence was not operating. However, failure to reject a strictly density-independent model is not strong evidence that density-dependence is not operating. If density-dependence is weak (or error variance is high), a non-linear recruitment function might be indistinguishable from a linear relationship (see Steele 1997). A more informative approach is to estimate and directly compare the magnitude of density-dependence in our two studies, rather than rely on separate null hypothesis tests (Osenberg et al. 1999). Because the studies differed in their design, we need to use two different forms of the Beverton-Holt model to estimate the strength of density-dependence (Bolker et al., in press). The Beverton-Holt model assumes that the per capita mortality rate is a linear function of cohort density:  $\mu = \alpha + \beta N$ , where  $\mu$  is the per capita mortality rate,  $\alpha$  is the density-independent mortality rate,  $\beta$  is the strength of density-dependence, and  $N$  is local fish density.

ty. This can be integrated to yield the recruitment function:

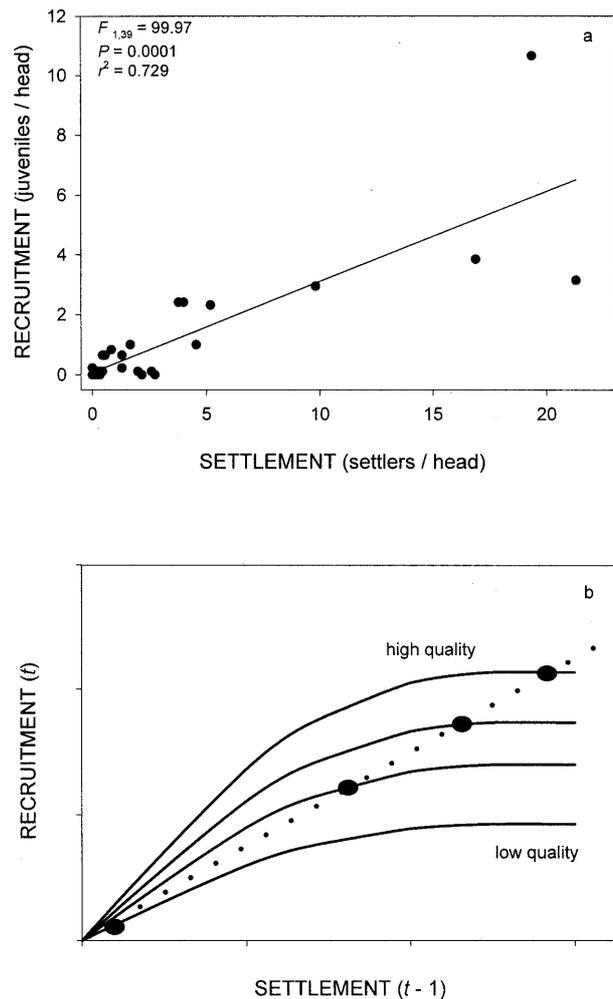
$$J_t = \frac{e^{\alpha t} S}{1 - \frac{\beta(e^{\alpha t} - 1)S}{\alpha}} \quad (2)$$

where  $J_t$  is the number of juveniles that survived from settlement (at age-0) to age- $t$ ,  $t$  is the age of juveniles (32 days in our study), and  $S$  is the initial number of settlers (see Bolker et al. in press). The  $\beta$ s in the differential and integrated forms of the model are the same, although different study designs require the application of one or the other form of the model to estimate  $\beta$ . Because  $\beta$  is a per capita effect, it also can be used to compare two studies that included slightly different ranges of variation in neighbor density.

In the experimental study, the densities of neighbor fish were held constant over 12 days. As a result, the targets experienced a relatively fixed neighborhood density, and we used the differential form of the model to estimate  $\beta$ . We assumed that fish density ( $N$ ) was equal to the number of targets plus neighbors (since adults and recruits had comparable per capita effects: Fig. 3), and then estimated  $\beta$  by regressing  $\mu$  (i.e., the reciprocal of mean longevity) against fish density for the five treatments:  $\beta$  was estimated to be  $-0.051$  ( $+0.0291$  95% CI) per day. In the observational study, fish density declined after settlement (dead fish were not replaced), so we fit the integrated form of the model to the data in Fig. 5a:  $\beta$  was estimated to be  $-0.00008$  ( $+0.0014$  95% CI) per day. Therefore, density-dependence was much stronger in the experimental study than in the surveys – the estimates differed by almost three orders of magnitude with no overlap in their confidence intervals. As a result, the disparity in our results was not due to a difference in statistical power, but was instead due to a true difference in the strength of density-dependence. What then, might have led to these differences? There are several possibilities.

The two studies were conducted in two different locations (patch reefs versus backreef), and different processes could be occurring in these two sites (i.e., different predator pressure and/or competition for resources). It is difficult to formally evaluate this possibility without additional data, but we think it is unlikely. For example, both sites are located within the same bay, have similar fish assemblages, and experience similar current flow, exchange of oceanic water (which is relatively low due to the barrier reef crest), and tidal influence ( $\sim 0.4$  m). In addition, the two sites are separated by only 300 m. This is approximately the size of our study site on the backreef, which was originally separated into blocks to test for spatial variation. We found no block effects, suggesting that there are not large differences in the processes acting on this spatial scale, at least within a habitat.

Another hypothesis is that experimental artifacts (i.e., tagging, handling, and stocking experimental fishes) may have caused greater density-dependence in our experiment (see Peterson and Black 1994). Indeed, survivor-



**Fig. 5** Recruit-settler relationships for **a** the observational study and **b** a graphical model developed to explain the apparent conflicting results of the observational and experimental studies. **a** The observed relationship between the mean number of juveniles produced from the mean of three settlement events (for three different time periods: June – July 1995, May – June 1996, and June – July 1996). Coral heads that were manipulated during the 1995 patch reefs experiment were not included in the regression analysis. The regression analysis was performed on square root transformed data, assuming a zero intercept. A non-linear model did not improve the fit. Back-transformed means are shown ( $n=39$ ). **b** A hypothesis in which coral heads vary in their quality (four possible levels of quality are shown). High-quality heads yield a greater number of recruits, and low-quality heads a lesser number, at any given initial density of settlers. The *dots* give proposed settlement rates to the different types of coral heads. If settlement is lowest to the low quality heads, then the overall pattern across heads can be a linear relationship, despite the curvilinear relationship within a category. The curvilinearity within a category indicates that per capita survival declines with settler density. The linear relationship across categories arises because survival is constant among the four coral types (the slope of the *dotted line* is equal to the probability that a settler survives to become a juvenile)

ship was lower for fishes in the experiment (see Results) compared to the observational study (Fig. 3). Handling probably increased overall levels of mortality, but it is not clear if handling interacted with density (as is required to explain the observed discrepancy in strength of

density-dependence between the observational and experimental study). If this hypothesis is correct, and tagging was the main cause of the density-dependence, then we would predict that the neighbors used in the experiment would exhibit reduced density-dependence. This prediction is not supported by the data – neighbors also showed evidence of strong density-dependent mortality (Fig. 4c). On the other hand, we only observed strong effects of experimental treatments from days 0–3, which might suggest that density-dependence only occurred during the “settling in” period, a period possibly associated with the most severe handling effects. However, recent observational studies have also suggested that density-dependence might act most strongly in the first few days after settlement (Schmitt and Holbrook, personal communication). This result is consistent with our experiment but free of any confounding influence of handling. As a result, there is little (or conflicting) evidence with which to evaluate the hypothesis that density-dependence was the result of an experimental artifact. It is a potentially important issue, which if supported, would cast doubt on a large amount of experimental data in the literature (Jones 1987; Forrester 1995; Steele 1997; Caselle 1999), and therefore demands further empirical evaluation.

The final hypothesis that we consider is that a confounding factor masked the effects of density-dependence in the observational study. Because the survey data were not from an experimental manipulation with random assignment of treatments, other factors could have co-varied with the number of neighbors. These factors could have affected the strength of density-dependence. For example, if coral heads differ in ways that affect survival, (e.g., higher food resources, fewer predators, etc.), then they could be grouped into classes based on these features. If survival on coral heads is density-dependent, as suggested by the field experiment, then each class of coral heads should exhibit a curvilinear (rather than linear) relationship between recruitment and settlement, but this relationship should differ among the classes: some coral heads offer greater per capita survival at a common density of settlers. If the recruitment function follows a Beverton-Holt relationship, then the overall height of each curve would be set by the features common to the class of corals. Thus, a patch reef (consisting of many types of coral heads) could be represented by a suite of density-dependent relationships, with each relationship corresponding to coral heads in a particular class (Fig. 5b). We refer to this difference among classes as variation in “quality”. This hypothesized pattern of correlation between settlement intensity and the strength of density-dependence could be due to inherent features of the coral head, its location, or the condition of larvae that arrive at that site (e.g., mean size or energy stores of settling larvae).

No matter what the underlying cause, this hypothesis requires that there be a positive correlation between quality (either of habitat or larvae) and the input of larvae (i.e., settlement). If settlement to coral heads was

random, then the observed pattern would be a fuzzy, curvilinear relationship with survival decreasing with settler density (e.g., “density-vague”, sensu Strong 1986). If, on the other hand, settlement was higher to high quality sites, then survival (assessed across the entire reef) could be independent of settler density (Fig. 5b), as we observed in our survey data (Figs. 3d, 5a). In this scenario, survival is density-dependent, yet it cannot be detected across sites due to the positive correlation between settlement and quality.

Although speculative, and we know of no other paper in the literature that suggests this scenario, our work has prompted a detailed analysis of “cryptic density-dependence” (a term coined by J. Shima, personal communication) using an existing observational data set (from Shima 2001). Shima and Osenberg (unpublished data) found no density-dependence when examining a large observational data set (as in Fig. 5a). However, when they subdivided reefs into discrete categories based on physical and biological variables, they found strong density-dependence within coral categories. Within each category, they fit a Beverton-Holt recruitment function, but the asymptote in these relationships (i.e., the strength of density-dependence) varied among the coral groups (as in Fig. 5b). Not only does their study provide further suggestion that this hypothesis may be of general relevance, but it also suggests that our discrepancy between observational and experimental results was not due to experimental artifacts – their entire data set was based on observational data. The salient issue may not be experiments versus observations, but rather homogeneous versus heterogeneous data sets: i.e., how much do corals (or larval groups) vary in “quality” within a study and is this variation associated with variation in settlement intensity?

The extent to which these interactions between settlement and density-dependence are of general importance is unknown, but will likely depend on the mechanism(s) that give(s) rise to positive correlations between settlement and habitat quality. We envision two basic hypotheses; one that involves passive processes and one that assumes active habitat choice by settling fishes. A passive mechanism might involve physical processes that influence both larval supply and habitat quality. For example, the distribution of fish larvae is influenced by local hydrodynamics (Roughgarden et al. 1988). Increased flow can also deliver greater amounts of zooplankton or nutrients to local sites. If the fishes consume the zooplankton, or other resources (such as algae) that are positively affected by the hydrodynamics, then there will be a positive correlation between settlement and habitat quality.

The other option is that fishes are capable of assessing the quality of a habitat and actively choose to settle in higher quality areas. For example, ideal free distributions (IFD; Fretwell and Lucas 1970) arise when individuals distribute themselves over the available living places or habitats in ways that maximize fitness. Habitat quality and the effect of density-dependence within each habitat jointly determine the selection of habitats by in-

dividuals (Fretwell and Lucas 1970). If variation in fitness were explained by variation in juvenile survival, then the IFD model would predict that settlers should distribute themselves to have equal survival probabilities across different sites (e.g., Fig. 5b). The IFD model can therefore explain the linear relationship between recruits and settlers (Fig. 5b), although it does not provide a mechanistic explanation for the pattern. Although we still know very little about larval behavior during settlement, it has been recently recognized that fishes are capable of far more complex behavior and “sampling” than previously believed (Ohman et al. 1998; Schmitt and Holbrook, personal communication). Insights from invertebrates may also be relevant. Pawlik (1992) suggested a scenario involving a “hierarchy of cues” that may be used by invertebrate larvae to first select generally favorable habitat and then to locate more specific settlement sites. Other groups are developing models to explore how larval condition (in terms of energy reserves) and different search patterns can result in a correlation between larvae condition and habitat quality (McEdward, personal communication). For example, if larvae can assess habitat quality, but those larvae in better condition (e.g., high energy reserves) are more selective because they have more time available to find suitable habitat before they exhaust their energy reserves, then average larval condition, habitat quality, and settlement intensity will all be correlated.

No matter which of the proposed hypotheses or mechanisms are involved, the disparity between the observational and experimental results is compelling, and we hope it stimulates further research. For example, one of the hypotheses we discussed above involves spatial variation in the strength of density-dependence. Although this has been discussed (e.g., Connell 1985), it is seldom investigated (but see Shima 2001). In addition, handling-induced density-dependence (another hypothesis discussed above) has never been tested in these systems, but if found, could undermine a wealth of existing studies that form a substantial part of the foundation for our current understanding of reef fish dynamics. Finally, the role of cryptic density-dependence has not been suggested previously, yet it has the potential to radically change the way we view coral reef systems. For example, many past studies that have taken an observational approach to study post-settlement density-dependence, have concluded that a linear relationship between recruitment and settlement demonstrates a lack of density-dependence (e.g., Meekan 1988; Doherty and Fowler 1994a, b; Williams et al. 1994). It is possible that these studies, in fact, have been conducted in systems with strong density-dependence that is obscured by variation in habitat quality (as suggested in our system). If so, then density-dependence may be more ubiquitous than previously believed. In addition, if this hypothesis is supported after further evaluation, it has the potential to integrate long-standing, but mostly disparate, interest in larval condition, habitat quality, and density-dependence.

Our study suggests the importance of conducting (and reporting) the results of both experimental and observa-

tional studies, which may require different quantitative tools to estimate the strength of density-dependence. Without the experimental study, we would have failed to detect density-dependence. However, without the observational data to compare to our experimental results, we would have overlooked the mismatch and therefore not have been forced to consider alternative hypotheses to explain the discrepancy between the studies. Our study demonstrates that no one single approach (or spatial or temporal scale) can fully explain factors affecting dynamics of reef fishes. Rather, study designs that incorporate different techniques to quantify the simultaneous effects of multiple factors will give us a more complete understanding of these complex systems.

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