Coral Reefs (1999) 18: 85–89

REPORT

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The influence of adult density on larval settlement in a coral reef fish, *Coryphopterus glaucofraenum*

Accepted: 30 October 1998

Abstract For marine species with open populations, patterns of larval settlement can have important consequences for performance and abundance at later life-stages. In this study, I tested whether larvae of a reef-dwelling goby (*Coryphopterus glaucofraenum*) settled differentially to reefs occupied by varying numbers of adults. I monitored settlement daily to reefs on which the density of adult gobies varied naturally, or was manipulated experimentally. Rates of settlement were constant across a broad range of adult densities, suggesting that larvae do not choose settlement sites based on the number of adults in their immediate vicinity.

Key words Larval settlement · Recruitment density-dependence · Reef fishes · Gobies

Introduction

Local populations of reef fishes, and many other marine species, are replenished when planktonic larvae (or sometimes juveniles) settle to the benthic habitat. Many studies of settlement have been motivated by its importance in population regulation. One key factor defining the influence of settlement on population dynamics is the nature of any interaction between settling larvae and established residents of the benthic habitat (Doherty and Williams 1988; Caley et al. 1996). Alternative models for the population dynamics of reef fishes predict different interactions between settlers and resident fishes. The recruitment limitation hypothesis predicts that resident fishes should not negatively influence larval settlement (Doherty 1981), whereas suppression of settlement by resident fish is one potential mechanism for competition in resource limitation models (Sale 1977).

For reef fishes, the process of settlement is difficult to observe directly because it happens sporadically and usually at night (Booth 1991; Sweatman 1985a; Sweatman and St John 1990; Robertson et al. 1988; Schmitt and Holbrook 1996; this study). Ecologists studying the replenishment of local populations have therefore usually measured recruitment rather than settlement, where recruitment is defined operationally as the number of recently settled juvenile fishes censused on the reef. Counts of established juveniles reflect both recent rates of settlement and any mortality that occurs between the time of settlement and the census. Consequently, when the interval between censuses of juvenile is long (weeks to months) the correlation between rates of settlement and recruitment may be low (Booth 1991; Levin 1994; but see Williams et al. 1994). Numerous experimental manipulations of resident density have shown that all possible influences of resident fishes on juvenile recruitment can occur: negative (Sale 1976; Shulman et al. 1983, Sweatman 1985b; Jones 1988; Forrester 1995; Tupper and Boutilier 1995), positive (Sweatman 1983, 1985b; Jones 1987; Booth 1992; Schmitt and Holbrook 1996) and no apparent effect (Williams 1980; Doherty 1983; Jones 1984, 1987; Levin 1993). In contrast to the numerous studies of recruitment, there have been few studies that have isolated the influence of resident fish on larval settlement (Shulman et al. 1983; Booth 1992; Tupper and Boutilier 1995, 1997; Schmitt and Holbrook 1996).

The paucity of research on this topic makes it impossible to assess the frequency of different types of interaction between resident reef fishes and settling larvae. Gregarious settlement is displayed by many different invertebrate taxa (Pawlik 1992) but, to date,

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the only reef fishes shown to exhibit this behaviour are damselfish in the genus *Dascyllus* (Booth 1992; Sweatman 1988; Schmitt and Holbrook 1996). No reef fishes, or benthic invertebrates, have yet been found to inhibit settlement by larvae of their own species (Woodin 1991), despite the fact that negative effects on recruitment are fairly common. In this study I provide a further test of the effect of adult density on the settlement of conspecific larvae in coral reef fishes. The study species is one for which the density of juveniles is negatively related to adult density (Forrester 1995), making it a good candidate to test for possible inhibitory effects of adults on settlement.

Methods

Study species

The study species, the bridled goby (*Coryphopterus glaucofraenum* Gill), is a small (maximum size approximately 70 mm in total length) benthic fish that is common throughout most of the Caribbean (Böhlke and Robins 1960). Bridled gobies typically occur on the sand around the edges of patch reefs, and in areas comprising a mixture of coral or rubble and sand. Adult gobies occupy small home ranges (< 2.5 m^2) within which they use crevices for shelter and feed on small benthic invertebrates in the sand. Their larvae spend an average of 27 days in the plankton, before settling to reef habitats (Sponaugle and Cowen 1994). Like most reef fishes (Booth 1991; Sweatman 1985; Robertson et al. 1988; Sweatman and St John 1990) they appear to settle mostly at night (see Results). Newly settled individuals are 8–12 mm in total length and are usually first seen on the sand within 0.5 m of a patch of reef or rubble (G. Forrester and M. Steele, unpublished data).

Experimental test for an influence of adults on settlement

I first tested for effects of adult gobies on larval settlement by manipulating goby density experimentally on isolated reefs constructed from natural materials. The reefs were constructed at a site adjacent to the southern side of Guana Island, British Virgin Islands (64°35′W, 18°29′N). Eight experimental reefs were constructed in a large sandy area, 5–6 m deep, from 12–14 August, 1995. The reefs were isolated by at least 10 m from each other, and any natural reef. They were constructed from coral and rubble transplanted from natural reefs nearby. Each experimental reef consisted of four square piles of coral and rubble (0.65 m on a side, 20 cm high) placed on the sand over a square of mesh, which helped prevent the rubble from sinking. Three of the piles formed an equilateral triangle around the fourth pile, which was in the centre of the triangle. The outer piles of rubble were 0.5 m from the central one, creating an area of roughly 8.5 m^2 within which larval gobies could settle (assuming they settle within 0.5 m of the reef).

The manipulation of adult gobies followed a regression design, with a different number of adult gobies transplanted to each of the eight reefs. This approach allowed me to define a quantitative relationship between adult density and larval settlement across a broad range of adult densities. To set up the treatments I collected adult gobies (> 25 mm total length) from reefs approximately 1 km from the study sites using anaesthetic (quinaldine) and hand nets. Adults were tagged by subcutaneous injection of acrylic paint (Lotrich and Meredith 1974) and then released on the eight reefs at densities ranging from 0.6 to 7.4 per m^2. Adults on natural reefs occurred within this range of densities in 90% of transects (area = 4 m^2, $N = 82$) censused around Guana Island in 1993 and 1994. The experimental treatment thus encompassed the typical range of adult densities, but higher densities (up to 15.5 per m^2) are occasionally observed (Forrester1995, unpublished data).

Adults were stocked from 14–18 August, and on 19 August I removed all juvenile gobies (<25 mm total length) from the reefs using hand nets to avoid confusing new settlers with older juveniles. Larval settlement to the reefs was monitored over the following 14 days, by making daily collections of newly settled gobies at dawn. I carefully searched the area within a distance of 1.5 m from the perimeter of each reef and used a hand net to remove all settlers that were encountered. Censuses of adult gobies on 23 Aug and 02 Sept indicated that adult densities remained at, or within 83% of, their initial levels throughout the experiment. Adults were also observed to establish home ranges, and commence spawning behaviour within a few days of stocking, suggesting that they behaved normally during the experiment. To determine the influence of adult density on settlement I regressed the density of adult gobies on a reef against the cumulative settlement (summed over 14 days).

Survey of settlement to reefs varying in adult density

As a second test for a relationship between the density of adult gobies and the rate of larval settlement, I monitored settlement on natural reefs which were occupied by different numbers of adults. These surveys provide evidence corroborating the experimental results, although it is possible that any correlation between adult abundance and settlement is spurious. I monitored settlement to unmanipulated habitats at two sites. The first was a set of six natural patch reefs located near Guana Island in the same sandy area used for the experiment. The reefs ranged in area from 2.8–4.1 m^2 and were isolated from neighbouring reefs by 7–14 m. The second site was a large area of mixed coral/rubble/sand habitat near Lee Stocking Island, Bahamas (23°46′N, 76°10′W). Here settlement was monitored to a set of 10 square plots (area = 2.25 m^2) demarcated at haphazardly selected locations within the expanse of habitat.

Settlement was measured at Guana island in 1996 (for 2 days) and 1997 (for 10 days), and at Lee Stocking Island in 1997 (for 7 days). Adult gobies occurred on the reefs/plots at densities from 0 to 6.22 per m^2, and densities remained stable within each study period (remaining between 92 and 105% of their initial level). Adult densities on the patch reefs at Guana Island were, however, poorly correlated between years ($r = 0.09$), which improved the chance that any observed relationship between settlement and adult density reflected a causal interaction.

Measures of settlement commenced on 7 October, 1996, and 18 June, 1997, at Guana island and on 23 August, 1997, at Lee Stocking Island. Juvenile gobies (< 25 mm total length) were removed from the reefs at Guana Island on the evening before monitoring of settlement began to avoid mistaking older juveniles for new settlers. This precaution was not taken during the later survey at Lee Stocking Island because it was determined that new settlers could be distinguished from older juveniles (based on their small size and pigmentation; G. Forrester and M. Steele, unpublished data). On subsequent mornings at dawn I searched the vicinity of each reef and removed all newly settled bridled gobies. At Guana Island, I collected settlers at dusk as well as dawn on six days in 1997, in order to determine whether any settlement occurred during the day. Linear regressions were used to test for a relationship between cumulative settlement to each reef and the density of adults.

Results

When settlers were collected from natural reefs around Guana island at both dawn and dusk, it was clear that most settlement during the 6 day period occurred after

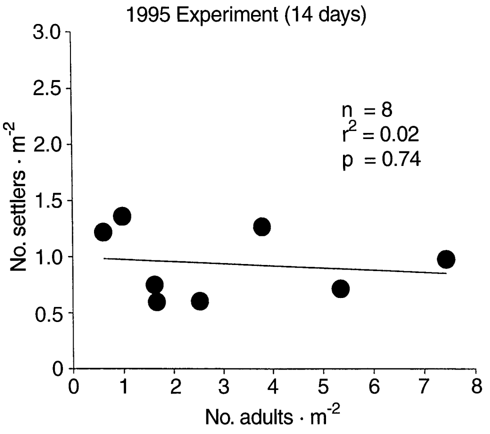

Fig. 1 The relationship between the density of adult bridled gobies stocked on isolated patch reefs and the cumulative settlement of larvae to those reefs. Settlers were removed from reefs daily over a period of 14 days

dark (total number collected at dawn = 32; number collected at dusk = 1). The overall rates of settlement differed among the three surveys and the experiment, being highest during the 1996 survey at Guana island and lowest during the experiment (Figs. 1 and 2). Daily settlement rates also varied within sampling periods (for example, 38% of the settlement in the 1997 Guana Island survey occurred on just one of 14 days).

In both the experiment (Fig. 1) and each of the three surveys of natural reefs (Fig. 2), regression analysis indicated no significant relationship between the number of larvae settling to a reef and the number of adults present. The lack of a significant relationship may be either because there really was no relationship, or because the test was not powerful enough to detect one. I used power analysis to help distinguish between these two alternatives. The test for the significance of a regression (H_0: slope of line = 0) is equivalent to the test for significance of the correlation coefficient (H_0: correlation = 0) (Cohen 1988). I therefore estimated the power of the regression analyses based on the degree of correlation between the two variables. Power analysis requires specification of the strength and sign (Woodin 1991) of relationship that one wishes to be able to detect, and a type I error rate. I chose a correlation coefficient (r) of –0.64, because this was the coefficient for the negative relationship between adult density and recruitment seen in previous work on bridled gobies (Forrester 1995), and used the conventional type I error rate of 0.05. Using these criteria, I had a 58% chance of detecting a significant relationship in the experiment. The chance of finding a relationship in each of the Guana island surveys was 43%, and power in the Lee Stocking survey was 69% (Cohen 1988). I know of no formal statistical procedure to combine the results of these power tests and calculate the overall chance of detecting a relationship. Taken together, however, I suggest that the consistent results of the four separate studies provide convincing evidence that larval settlement in bridled gobies is independent of the local density of adults.

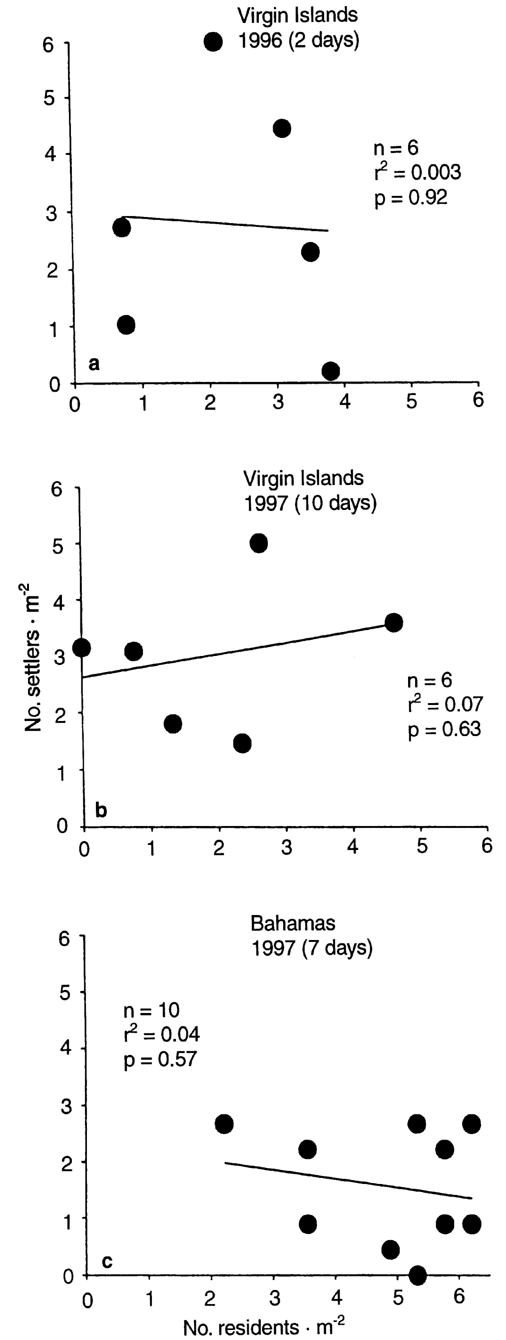

Fig. 2a–c Relationships between the density of adult bridled gobies in natural habitats and larval settlement to those habitats. Settlement was measured on **a–b** isolated patch reefs or **c** plots within an area of continuous habitat. Settlers were removed from reefs daily and the data presented are the total number of settlers removed over **a** 2 days **b** 10 days or **c** 7 days

Discussion

Varying responses of settling larvae to adult conspecifics

The extensive variation in settlement among the three surveys and the experiment, and the day to day variation within each component of the study, are typical of reef fishes studied to date (Doherty and Williams 1988). The differences in settlement rates among the surveys and the experiment are not surprising because the various components of the study were done under a wide range of conditions. Notably, settlement was measured in different geographic locations, in different microhabitats, in different years, and during different lunar phases, all factors known to be associated with variability in settlement rates (Doherty and Williams 1988; Sponaugle and Cowen 1994). Other research on bridled gobies indicates that the range of variation in settlement recorded in this study is typical for this species, both on natural reefs and artificial substrata similar to the experimental reefs (G. Forrester and M. Steele, unpublished data).

The results of this study suggest that settlement of bridled gobies is independent of the number of conspecific adults present, at least over distances of a few to tens of metres. Relatively few other studies have performed similar tests, so the prevalence of different sorts of settlement patterns in response to adults is difficult to judge for reef fishes. Many different invertebrate taxa show gregarious settlement patterns (Pawlik 1992), but the only reef fishes that have so far shown this behaviour are three species in the genus *Dascyllus*. *Dascyllus albisella* and *D. aruanus* both settle in greater numbers to habitat occupied by established conspecifics than to unoccupied habitat (Booth 1992; Sweatman1988), and larval *D. albisella* also settle preferentially where there are few, rather than many, residents (Booth1992). Interestingly, Schmitt and Holbrook (1996) examined settlement responses of *D. trimaculatus* to a continuous range of resident densities, and showed that although settlement initially increased with increasing resident density, it then declined as the number of inhabitants increased to very high levels. In this study I examined settlement to a range of adult densities within which greater than 90% of adult gobies at the two study sites occur (up to 7.5 m^{-2}). Densities twice as high as this are occasionally observed (G. Forrester and M. Steele, unpublished data), so the possibility that adults might inhibit settlement at extremely high levels of adult density remains untested. Apart from studies on *Dascyllus*, the influence of adults on settlement has been tested for only one other species of reef fish, *Tautogalabrus adspersus*, a wrasse that inhabits cold-temperate rocky reefs. Like the bridled goby, *T. adspersus* showed no differences in settlement to reefs occupied by varying numbers of adults, even with adults at unnaturally high densities (Tupper and Boutilier 1995, 1997). Even though positive influences of residents on settlement are common, no reef fishes or benthic marine invertebrates have yet been shown to inhibit settlement by larvae of their own species at all densities (Woodin 1991). Many benthic invertebrates (Woodin 1991), and some adult damselfish (Shulman et al. 1983; Sweatman and St John 1990) do, however, suppress the settlement of other species in their vicinity so the potential for adults to inhibit settlement by conspecific larvae does exist.

Clearly, further studies are needed to reliably define the range of responses displayed by settling reef fishes to conspecifics. Future work should also focus on testing hypotheses about potential reasons why settling larvae might avoid, or be attracted to, members of their own species. Two obvious differences among the species tested to date occur in their microhabitat affinities, and their social systems. The three *Dascyllus* species occur in tightly organized social groups, whereas *C. glaucofraenum* and *T. adspersus* occupy individual home ranges. The three *Dascyllus* also occur in quite specific microhabitats that are distributed in discrete patches, whereas *C. glaucofraenum and T. adspersus* show less specific microhabitat affinities and have less clumped distributions. Such differences among species are most likely to be important if they influence future prospects of surviving and successfully reproducing. For the *Dascyllus* species that settle gregariously there are some subsequent costs in the form of reduced early growth and survival (Jones 1987, 1988; Forrester 1990, Booth 1995), though the consequences during adulthood have not been explored. A previous study of bridled gobies reported a negative relationship between adult density and the accumulation of recruits on isolated patch reefs (Forrester 1995). Given that settlement in the present study was density-independent, the density-dependent recruitment seen previously must result from poor survival of newly settled gobies on reefs with high densities of adults. The survival of adult bridled gobies is also much lower on reefs where they are at high densities (Forrester 1995, unpublished data). This pattern of survival suggests that a bridled goby choosing to settle where members of its own species abound has a much worse chance of surviving to reproduce than one settling on a sparsely populated reef. This raises the question, why not avoid settling where there are many conspecifics?

One possibility is that there may be benefits of settling to high density areas, which counterbalance the reduced probability of survival. An alternative, more proximate explanation is that larval gobies may simply be unable to detect adults on the reef. *Dascyllus* larvae are able to detect chemicals released by reef-dwelling conspecifics (Sweatman 1988), but artificially reared anemonefish larvae are apparently unable to do so (Elliott et al. 1995). Whether larvae of bridled gobies, or other species, can detect adults of their own species, and use this information to assess local adult density is unknown. Larvae of some reef fishes can apparently use chemical cues to discriminate among benthic microhabitats (Carr 1991; Elliott et al. 1995) so further studies may reveal responses to adult fishes.

Acknowledgements Many thanks to Ian Greenspan, Amy Karpenske, Elizabeth Kintzing, Yuri Springer, Julie Standish, and Mark Steele for help with field work, and to Lianna Jarecki and the staff at Guana Island and Lee Stocking Island for excellent logistical support. Financial support from NSF (OCE 9618011), the Falconwood Corporation, and Guana Island Wildlife Sanctuary is gratefully acknowledged.

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