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Settlement and recruitment of three damselfish species: larval delivery and competition for shelter space

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Abstract Spatial patterns of settlement and abundance of older life stages were examined for three species of damselfish in the genus Dascyllus by monitoring natural colonization of standard amounts of initially empty juvenile microhabitat (anemones for D. trimaculatus; branching coral for D. flavicaudus and D. aruanus) transplanted to a series of sites within lagoons of Moorea, French Polynesia. Large spatial differences in larval colonization were observed, which were temporally consistent but different among the species. At the whole-island scale, D. trimaculatus settled primarily on the northern shore, while settlement of the other two species was greatest at the southern end. The three species also showed different patterns of settlement within lagoons: D. aruanus settled mainly nearer to shore, D. flavicaudus primarily on offshore lagoon portions and D. trimaculatus colonized equally across the lagoons. Among sites around the island, the relative abundance of older juveniles after 10 months was a curvilinear function of the relative abundance of settlers for two species (D. trimaculatus and D. flavicaudus). There was no relationship between patterns of settlement and abundance of older juveniles for D. aruanus, although juvenile abundance was inversely related to that of juvenile D. flavicaudus. At the within-lagoon scale, settlement mirrored almost exactly the relative abundance of older lifestages of D. trimaculatus and D. flavicaudus, whereas there was just a qualitative match for D. aruanus. A competition experiment revealed that juvenile D. flavicaudus had a greater effect on population growth of D. aruanus than vice versa, and this mechanism helped explain why the modification of settlement patterns was greatest in D. aruanus. Interspecific variation in abundance of older stages was shaped to differing extents by both patterns of larval delivery and subsequent density-dependent processes involving competition for shelter space.

Key words Post-settlement processes · Competition · Recruitment · Settlement · Dascyllus

Introduction

A fundamental question for species with demographically open populations is what causes spatial variation in abundance. This issue has been addressed extensively in benthic marine systems because most species have early developmental stages that disperse in the plankton. Work on marine organisms has revealed two broad classes of processes that shape local patterns of abundance: those processes that affect the input of planktonically dispersed young to a reef (settlement; see Keough and Downes 1982), and those that subsequently modify settlement patterns. There are at least three general factors that can affect input: physical transport, larval behavior, and availability of settlement habitat. Spatial variation in such physical oceanographic features as currents creates variability in the delivery of propagules, which can be detected in patterns of abundance of older life stages (Grosberg 1982; Gaines et al. 1985; Raimondi 1988, 1990, 1991; Kingsford 1990; Fowler et al. 1992; Milicich et al. 1992; Wellington 1992; Caselle and Warner 1996; Sponaugle and Cowen 1996; Jones 1997). Many larvae are not passive particles (Leis et al. 1996; Leis and Carson-Ewart 1997) and their behavior can influence the time, location, and/or intensity of settlement. Indeed, larval behavior has been implicated as a factor affecting distribution or abundance of older life stages on several spatial scales (Grosberg 1982; Keough and Downes 1982; Raimondi 1990; Milicich et al. 1992; Wellington 1992; Tolimieri 1995; Caselle and Warner 1996; Doherty et al. 1996; Schmitt and Holbrook 1996; Sponaugle and Cowen 1996; Jones 1997). Finally, variation in the availability of suitable settle-
ment or nursery habitat is known to influence the intensity of colonization (Carr 1994; Caselle and Warner 1996; Schmitt and Holbrook 1996).

Post-settlement processes, including mortality after colonization and local movement of older stages, can alter qualitatively patterns of relative abundance that originate at settlement if they operate in a density-dependent fashion (Jones 1987, 1991; Forrester 1995; Caley et al. 1996; Schmitt and Holbrook 1999). While density-dependent mortality has been observed more often for sessile marine species than for mobile species, there is growing evidence that per capita death rates of juvenile reef fishes can increase with density (Forrester 1995; Hixon and Carr 1997; Steele 1997; Schmitt and Holbrook 1999), especially during the period immediately after settlement (Schmitt and Holbrook 1999).

Nonetheless, it is widely held that the input of larvae of reef fishes to a reef typically is too low for local resources to be depleted and that therefore competition will be absent or weak. As a consequence, local losses will be independent of density (Doherty 1991; Robertson 1988, 1992). This “recruitment limitation hypothesis” holds that spatial variation in the distribution and abundance of reef-associated life stages will directly reflect patterns of larval supply (e.g., Doherty and Fowler 1994).

One difficulty in evaluating the causes of variation in abundance of reef fishes is that studies tend to examine either a particular subset of life stages (e.g., larvae to early juvenile, juvenile to adult), a general process (e.g., larval supply, post-settlement mortality) or a specific mechanism (e.g., predation), and are often focused at a single spatial scale. The lack of studies that simultaneously consider multiple life stages and processes across spatial scales hinders our ability to draw general conclusions about the roles various factors play in shaping patterns of abundance. Further, insight can be gained by considering multiple species concurrently as this can help identify reasons for similarity or difference in responses among species. Here we examine patterns of settlers and of older life stages of three species of damselfish in the genus Dascyllus at two spatial scales to explore: (1) interspecific patterns of settlement (larval supply), (2) the contributions of settlement and post-settlement processes to shaping patterns of abundance of older life stages, and (3) the existence and influence of intra- and/or interspecific competition. The two spatial patterns considered in the lagoons of Moorea, French Polynesia were among lagoons around the island perimeter (i.e., island-wide patterns) and between nearshore and offshore portions within lagoons.

Materials and methods

The system

Field work was conducted in Moorea (17°30′0″S:149°50′W), French Polynesia, a triangular island with a coastline perimeter of about 60 km. A barrier reef encircles the island, forming a narrow lagoon system 0.8–1.3 km wide and ~5–7 m deep (for more details, see Galzin and Pointier 1985). On each of the three sides of the island, the barrier reef is cut by three to five passes. Water mainly enters the lagoons over the crest of the barrier reef and exits through the passes. The bottom in the lagoons is composed of patch reefs interspersed with sand.

Three species of Dascyllus are among the most common damselfish on Moorea: the three-spot dascyllus (D. trimaculatus), yellow-tailed dascyllus (D. flavicaudus), and humpback dascyllus (D. aruanus) (Galzin 1987a,b). These diurnal planktivores lay benthic eggs; larvae hatch and enter the plankton after ~3 days (Garnaud 1957; Thresher 1984), settling back to the reef after about 22–24 days (Brothers et al. 1983; Wellington and Victor 1989; M. Kingsford, S.J. Holbrook and R.J. Schmitt, unpublished work). The species show the same temporal patterns of settlement at Moorea. Reproduction and settlement occur throughout the year, but are greater during the Austral winter period of June–August when approximately half of all Dascyllus young that colonize over the year settle (Schmitt and Holbrook, in press). There is strong lunar periodicity in settlement, which typically occurs in distinct 3- to 5-day-long pulses twice a lunar month around the time of the first and third quarter moon phases; little or no settlement occurs during the intervening days (Holbrook and Schmitt 1997; Schmitt and Holbrook, in press). During a settlement pulse, maximum arrival of each species typically was within a day of the other species (Schmitt and Holbrook, in press).

D. trimaculatus settle to sea anemones (mainly Heteractis magnifica on Moorea; Dunn 1981; Fautin 1985; Fautin and Allen 1992) where they remain throughout the juvenile phase; adults are free-living and do not shelter on anemones. D. flavicaudus and D. aruanus settle to and remain on live branching corals (Sale 1971; Forrester 1990; Allen 1991). In Moorea, these two species mostly settle to Pocillopora spp, but other corals (Acropora spp., Montipora spp.) also can be occupied.

Operational conventions and estimation of settlement

We operationally defined settlement as the appearance on a microhabitat (anemone or coral) of a new colonist that was observed within 12 h of its arrival from the plankton (Schmitt and Holbrook 1996, 1999). Newly-settled Dascyllus were morphologically quite distinct from individuals that had been on the reef for >1 day (Holbrook and Schmitt 1997). Settlement was estimated from daily counts of new arrivals on a standard amount of microhabitat to remove the influence of spatial variation in useable habitat. Settlement occurred at night, and in situ infrared video of settling D. trimaculatus indicated that larvae colonized the reef primarily between 00:00 and 05:00 hours (Holbrook and Schmitt 1997, in press). Daily counts of fish were begun by 08:00 hours and generally were completed by ~12:00 hours.

Because we wanted to isolate the effect of variation in larval supply, we used standardized amounts of appropriate settlement microhabitats from which resident fish were removed to eliminate the influence of spatial variation in useable habitat and reduce potential priority effects on settlement. As a result, we assume that daily counts of new settlers to initially empty microhabitats provide an estimate of larval supply, although it not only will reflect variance in the local flux of competent larvae but also variance in local conditions that influence per capita settlement rates. However, the effect of local conditions on our estimate of larval supply is greatly reduced by the use of standardized settlement habitat and from the removal of residents that could influence the probability a larva will settle (Sweatman 1983, 1985).

Island-wide patterns

Island-wide patterns of settlement were estimated by monitoring natural colonization to standard amounts of microhabitat transplanted to nine sites. The sites were located on sand bottom at 4–5 m depth, halfway between the shore and the barrier reef, positioned similarly with respect to proximity to reef passes. Sites were
isolated from naturally-occurring microhabitats suitable for Dascyllus. At each site, ten live Pocillopora and ten anemones were transplanted to cinder blocks set 5 m apart on the sand in two parallel rows. Corals were approximately 30 cm diameter and 20 cm in height, while anemones were 25–30 cm in diameter. Each coral was affixed to a cinder block using Z-Spar (Splash Zone Compound), while anemones were allowed to attach naturally to the blocks. The resultant density of transplanted microhabitats (~10 per 50 m² of reef) was near the upper range of their natural densities in the lagoons of Moorea. A tenth, inshore site was set up in an identical fashion at the same time, and monitored concurrently with the nine mid-lagoon sites; this inshore site was not used in analyses of island-wide settlement patterns, but was included in analyses of settler-recruit relationships.

Just prior to expected pulses of settlement, all resident fish were removed from corals and anemones by divers using hand nets. Subsequently, newly settled individuals were counted daily for a 2-week period that started 2–4 days before heavy settlement began. This was done twice during the Austral winter season (August 1996 and July 1997). To test whether settlement deviated from uniform among the sites, single-classification goodness-of-fit tests were calculated for each species with each site having an expected frequency of one-ninth (there were nine sites) of the settlers in a given pulse. Evenness was calculated for each settlement pulse and for the cumulative number of settlers in both pulses. Since the overall amount of settlement differed among the species and between the two settlement cycles, relative abundance was used to facilitate cross-species comparisons. For each species, the fraction of all settlers that colonized each site in a 2-week period was calculated by dividing the cumulative number of settlers at a site by the cumulative number at all nine sites for that observation period. (Note that microhabitats within a site are not replicates as the number of individuals on the ten corals or anemones was summed to obtain one value for a site.) The two pulses served as replicates to calculate the mean fraction of a species that colonized each site. Site means were used to calculate correlations of island-wide settlement for each pairwise combination of Dascyllus.

No suitable habitat for Dascyllus existed naturally near the lagoon sites, precluding comparison of settlement patterns with natural patterns of abundance of older life stages at this spatial scale. Instead, we allowed fish to accumulate for 10 months on initially empty transplanted microhabitats at the nine mid-lagoon and one inshore sites. We did this for two different 10-month periods: September 1996–June 1997 and again from September 1997–June 1998. In both cases, the exact same locations and microhabitats were used, and the methodology used was identical except for one detail. For the first 10-month period, new colonists from the settlement pulse that was monitored daily were left on the microhabitats, whereas the initial settlement cohort for the second 10-month period was not estimated from daily counts. Importantly, the number of settlement pulses over which fish accumulated was the same in both cases. In late June of 1997 and 1998, the number of Dascyllus that had accumulated was counted. For analyses, we excluded individuals from the most recent settlement pulse, and we refer to these fishes > 2 weeks (and < 10 months) post-settlement as “older juveniles.” The standardized abundance of older juveniles among the sites was compared with the mean proportion of settlers among the sites as estimated from the two sets of daily counts. Note that these are not true cohort analyses (i.e., settlers vs surviving juveniles from that settlement cohort) because the older juveniles consisted of multiple age classes. The distribution of body sizes of these accumulated, older juveniles indicated that they accrued from several different settlement pulses. However, per capita mortality of each species at Moorea is strongly density-dependent only during the first few weeks after settlement (Schmitt and Holbrook 1999).

Thus, we are comparing the pattern of settlement with that of fishes that have made it through the period when losses are most strongly affected by density.

For each species, linear and non-linear regression models were fitted to the standardized abundances among sites at settlement and of older juveniles after 10 months. The variable in the non-linear model was the log[standardized abundance of settlers]. Caution must be exercised when employing this kind of approach for a cohort as the number of survivors to some period cannot exceed the number of initial settlers (McGuinness and Davis 1989). Here, however, we used the standardized abundance of settlers estimated from two different settlement cycles as an index of settlement to predict the standardized abundance pattern of older juvenile age classes that accumulated over ~20 settlement cycles.

Differences between our index of settlement and the standardized abundance of accumulated, older juveniles could have resulted from qualitatively different patterns of settlement among the sites over the 10-month period compared with the two cycles for which settlement was estimated daily. To examine temporal consistency in the pattern of settlement among the sites, we estimated the number of settlers to these sites for four additional 2-week long settlement cycles. These additional surveys were done in July 1996, and during July and August 1997. At the initiation of observations every 2 weeks thereafter, resident fish were removed from all transplanted microhabitats. The numbers of new colonists were counted weekly rather than daily as before. This technique underestimated the actual number of settlers as only survivors to each census date were counted, and more importantly, it introduced bias as early mortality of these species is strongly density-dependent (Schmitt and Holbrook 1999). The bias is relatively greater underestimate of the actual number of settlers at higher than at lower densities. For our purposes, the bias is conservative as it will tend to weaken a positive correlation between the two estimates of spatial variation in settlement. Correlations were calculated between the mean standardized abundance of settlers among the sites for the two types of estimates of settlement patterns.

D. flavicanthus and D. aruanus both settled to the same transplanted coral heads and the potential effect of variation in density of the congener on the abundance of fish at 10 months was explored statistically. For each of these species, variation in abundance of older juveniles among the ten sites that could be attributed to settlement was removed by obtaining residuals from the relationship for a species between the absolute abundance of settlers and older juveniles. The residuals, which represented the expected abundance of fish at a site if settlement of that species had been uniform among the sites, were then regressed against the density of older juveniles of the congener at the sites. Since we were interested in the extent to which the abundance of the congener at a site was related to the (residual) abundance of the focal species (i.e., after variation attributable to settlement was removed), we calculated correlation coefficients. The slope of the relationship is an estimate of the effect of one species on the abundance of the other.

Within-lagoon patterns

To examine patterns of settlement with respect to proximity to the barrier reef and shore, four additional sites were established in two lagoons (one on the north and the other on the west shore of Moorea). In each lagoon, one site was close to shore and the other was in the offshore half. At each site, anemones and Pocillopora were transplanted as described above, although at both inshore locations, anemones were attached to natural patches of hard substrate rather than to cinder blocks. For the pair of sites on the north shore, 40 anemones and 40 corals were transplanted to each site, whereas 10 of each microhabitat type were transplanted to each of the sites on the west shore. For statistical analyses, data were expressed as the number of settlers per ten microhabitat units. Fish on all microhabitats were removed just prior to the start of observations, and the number of new settlers on each microhabitat was counted daily for a 2-week period that encompassed a settlement peak. This was done once in August 1996 and a second time in July 1997. For each species, data were analyzed by two-way ANOVA with lagoon location (inshore, offshore) and year (1996, 1997) as the factors.

Our experimental design described above confounds location effects with substrate type, but naturally-occurring anemones have
a lower loss rate than transplanted individuals. To assess possible bias, we conducted a preliminary experiment comparing settlement of *D. trimaculatus* to anemones on natural substrate and cinder blocks. Daily counts were made over a 10-day period of settlement of *D. trimaculatus* to seven naturally-occurring anemones on a series of local patch reefs and to individuals of the same size transplanted to ten cinder blocks that were interspersed haphazardly on reefs among the natural anemones. There was no statistical difference in the number of settlers between the two groups ($t_{14} = 0.10; P > 0.9$) and the means differed by just 7%.

Patterns of settlement between inshore and offshore locations in the two lagoons were compared with the pattern of relative abundance of older life stages that occurred on natural habitat. To estimate the standardized abundance of older life stages, four lagoons (including the two where settlement patterns were estimated) were divided into inshore and offshore halves, and band transects, each $5 \times 40$ m, were randomly positioned on reefs that contained suitable habitat for each lagoon half. Fish and the amount of suitable habitat were enumerated in a minimum of four transects in each half of each lagoon. Suitable habitat was estimated as the volume of the species of branching coral occupied by *D. aruanus* and *D. flavicaudus*, or the oral surface area of anemones for *D. trimaculatus*. The height, width, and length of each appropriate coral or anemone measured on a transect were used and the approximate shape of the head noted (e.g., hemispheric) for calculation of total volume. The total volume (corals) or area (anemones) of each microhabitat on a transect was our estimate of useable habitat. For each species, the number of individuals older than the most recent settler cohort was divided by our measure of the amount of suitable habitat in the transects for each lagoon half to remove differences in relative abundance due to habitat availability. The fraction of older individuals (per unit microhabitat per species) found on inshore and offshore halves of each lagoon was estimated, and the mean fractions were calculated using the four lagoons as replicates. When the relative abundance of older life stages of a species at this spatial scale appeared to differ from the pattern of settlement, statistical differences were explored using a t-test on the proportions (arcsin transformed) of settlers and older individuals on the inshore lagoon half (with lagoons as replicates).

Competitions between the young of *D. flavicaudus* and *D. aruanus*

We conducted a competition experiment in the field to test whether interactions between the young of *D. flavicaudus* and *D. aruanus* affected their population growth rates. The null hypothesis was that the interspecific competition coefficients were both 0 (i.e., $a_1$ and $a_2 = 0$), that is, an individual of each species would have no effect on the per capita population growth rate of the other. We did not investigate intraspecific density effects. The experiment was done in the lagoon on the north shore of Moorea where both *D. flavicaudus* and *D. aruanus* settled commonly. At that site, *Pocillopora* heads were affixed singly to cinder blocks as described above and placed on sandy bottom in three parallel rows with a minimum separation of 5 m between adjacent corals. Immediately prior to the start of the experiment, resident fish on the corals were removed. Individual *D. flavicaudus* and *D. aruanus* that had settled ~1 week previously were isolated from other areas and after a brief period (~5 days), in the laboratory, were outplanted to the corals according to three randomly-assigned treatments: (1) eight *D. flavicaudus*, (2) eight *D. aruanus* and (3) eight of each species (i.e., 16 fish total). The targeted density of young (eight per coral per fish species) was above the mean observed for single settlement cycles at nearby sites (~4–6 per coral), but was far below the maximum density of juveniles observed on corals nearby. There were 10 replicate corals for each of the single species treatments and 20 replicate corals for the combined species treatment. No attempt was made to adjust densities after the initial stocking.

Some corals in all treatments lost fish in the first 24 h after stocking, which presumably reflected the influence of handling. Accordingly, we only followed corals that had lost two or fewer fish 1 week after corals were stocked. This resulted in 14 replicates for the combined species treatment, 9 replicates of the *D. aruanus* treatment, and 5 replicates of the *D. flavicaudus* treatment. The average number of fish at the start of the experiment (1 week after stocking) was 7.4 fish (per species) per coral, although both single-species treatments had slightly greater initial numbers (*D. aruanus*: 7.6, *D. flavicaudus*: 8.3) than the combined species treatments (*D. aruanus*: 6.2, *D. flavicaudus*: 7.5). The experiment ran for 72 days, at which time the number of fish on each coral was counted. For each coral, the fractional change in population size of a targeted species over the 72 day period was calculated as ($n_{final} - n_{initial}$)/($n_{initial}$). The data for each species were analyzed by one-way ANOVA.

### Results

**Island-wide patterns**

The total amount of settlement of each species differed by 20–50% between the two settlement cycles at the nine sites where daily counts were made. On average, *D. trimaculatus* had the greatest density of settlers (~41 settlers per site per pulse), *D. flavicaudus* had the next most (~37 per site per pulse), and *D. aruanus* showed the lowest settlement (~20 per site per pulse). Settlement of each species was highly non-uniform around Moorea (*Fig. 1, Table 1*), and the strong positive correlation in settler densities between the two pulses for each species suggested this pattern may be temporarily consistent (*D. trimaculatus*: $r = +0.75$; *D. flavicaudus*: $r = +0.79$; *D. aruanus*: $r = +0.87$; $n = 9$). Because the spatial patterns of settlement did not differ qualitatively between the two pulses for any species, temporal variation did not drastically reduce the amount of spatial variation in the cumulative input of colonists among the sites (Table 1).

The three species did not show the same spatial variation in settlement, and two qualitatively different patterns of colonization were discerned at this spatial scale (*Fig. 1*). Settlement of *D. trimaculatus* was greatest at the northern sites, with >80% of settlers colonizing the five most northern sites (sites 1, 2, 3, 4 and 9: *Fig. 1*). By contrast, settlement of *D. flavicaudus* and *D. aruanus* was greatest at the southern end of Moorea. More than 45% of the settlers colonized the two most southern locations (sites 6 and 7: *Fig. 1*). There was a strong, positive correlation in the settlement of *D. flavicaudus* and *D. aruanus* among sites ($r = +0.88$; $P < 0.005$), but weak, negative correlations between settlement of these species and that of *D. trimaculatus* with *D. flavicaudus* (*D. flavicaudus*: $r = -0.24$; $P > 0.5$; with *D. aruanus*: $r = -0.33$; $P > 0.35$).

After 10 months, a signal of settlement was apparent in the spatial distribution of older juveniles among the study locations for two of the three species in both years (*Fig. 2*). For *D. trimaculatus* and *D. flavicaudus*, the mean fraction of older juveniles at 10 months scaled positively among sites with the relative abundance of settlers, whereas there was no apparent relationship between the relative abundance of *D. aruanus* settlers and recruits at this spatial scale (*Fig. 2*). A semi-log
model provided significantly better fits to the data for both years for *D. trimaculatus* (1996–1997 and 1997–1998: curvilinear: $r^2 = 0.97$ and 0.79; linear $r^2 = 0.90$ and 0.69; $n = 10$) and especially for *D. flavicaudus* (1996–1997 and 1997–1998: curvilinear: $r^2 = 0.80$ and 0.71; linear $r^2 = 0.53$ and 0.45; $n = 10$). The semi-log model also had a similar effect for *D. aruanus* (1996–1997 and 1997–1998: curvilinear: $r^2 = 0.18$ and 0.17; linear $r^2 = 0.11$ and 0.07; $n = 10$), although neither model was statistically significant for either year. The relationships for each species were remarkably consistent between the two years (Fig. 2).

The curvilinear relationship between settlers and older juveniles could have arisen from the operation of density dependence or from temporal variation in the spatial pattern of larval supply that resulted in a time-averaged delivery of potential colonists that was far more uniform among sites than any single pulse. We tested the latter possibility by comparing the spatial patterns of settlement from the two pulses for which settlers were counted daily with four additional pulses where settler abundance was estimated weekly. There were strong, positive correlations in the pattern of among-site settlement for the two types of estimates ($+0.80$ for *D. trimaculatus*, $+0.95$ for *D. flavicaudus*, and $+0.93$ for *D. aruanus*), and highly significant concordances in the ranking of sites among the six pulses (Kendall’s $W$: *D. trimaculatus* $= 0.63$; *D. flavicaudus* $= 0.79$; *D. aruanus* $= 0.77$; $P < 0.001$ in all cases). These analyses suggested that patterns of larval delivery around the island were temporally quite consistent among at least six different lunar settlement pulses. Coefficients of variation in the cumulative number of settlers among the sites from all six pulses were not substantially lower than estimates from single pulses (Table 1), further suggesting that the time-averaged spatial variation in larval supply was not more uniform than for individual pulses.

*D. aruanus* and *D. flavicaudus* occupied the same corals, and patterns of abundance of recruits among the sites could have been influenced by interactions between these species. After the effect of variation in settler density was removed, each species displayed a negative relationship between its abundance at a site after 10 months and the density of older juveniles of the congener (Fig. 3), although only three of the four correlations were statistically significant. Variation in the density of the congener explained 30–45% of the variation in abundance of older stages that was not attributable to patterns of settlement. The slope of the relationship is an estimate of the per capita effect of one species on the growth of the other, and for these data sets, no slope was statistically different from any other.

Within-lagoon patterns

Within-lagoon patterns of settlement were consistent between inshore and offshore locations in both years examined (i.e., non-significant location × year interaction terms; Table 2). The species of *Dascyllus* displayed three different patterns of settlement at this spatial scale. *D. trimaculatus* had an equal fraction of settlers colonizing nearshore and offshore locations (Fig. 4, Table 2). By contrast, the remaining two species displayed strong but complementary settlement patterns. More than 80% of the *D. flavicaudus* settlers colonized the offshore locations, whereas almost 70% of *D. aruanus* settled to the nearshore sites (Fig. 4, Table 2).
Within-lagoon patterns of settlement into experimental microhabitats of *D. trimaculatus* and *D. flavicaudus* almost exactly mirrored the pattern of relative abundance of older stages on natural microhabitats (Fig. 4). While there was a qualitative agreement for *D. aruanus* – most settlers and most older stages occurred inshore – the relative abundance of older life stages offshore (14%) was less than half that expected based on settlement (31%; Fig. 4), a difference that was statistically significant (*P* < 0.05).

Competition between the young of *D. flavicaudus* and *D. aruanus*

In the absence of *D. aruanus*, the population of juvenile *D. flavicaudus* increased by an average of 25% over a 3-month period (Fig. 5). The rate of growth of *D. flavicaudus* populations was not statistically affected by the

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<th>Damselfish species</th>
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Table 1. Single-classification goodness-of-fit tests (G-test) for deviations from uniform settlement of *Dascyllus trimaculatus*, *D. flavicaudus* and *D. aruanus* among nine mid-lagoon sites distributed around the 60-km perimeter of the island of Moorea, French Polynesia (see Fig. 1). G-tests were calculated separately for the two pulses for which the number of settlers was estimated from daily counts (“daily” pulse), for the cumulative number of settlers in both pulses estimated from daily counts, and for the cumulative number of settlers estimated from six pulses (the two “daily” counts and four others where settlers were estimated from weekly counts). Expected frequencies of settlers were computed as 1/9th of the total number of settlers in a pulse or the cumulative number in both pulses (i.e., uniform settlement among the nine sites); all χ² values were significant at *P* < 0.001. Coefficients of variation for spatial patterns of settlement among the sites are given in parentheses under the χ² value.

Fig. 2 Relationships between the proportion of settlers (estimated from two settlement cycles) and proportion of older juveniles that accumulated over two 10-month periods (1996–1997 and 1997–1998) among lagoon sites. The inshore site not included in Fig. 1 is denoted by a solid triangle (note that since the proportion of settlers is based on ten sites, the value for a site is not identical to its value in Fig. 1). Semi-log model fits and equations are shown when significant.

Within-lagoon patterns of settlement into experimental microhabitats of *D. trimaculatus* and *D. flavicaudus* almost exactly mirrored the pattern of relative abundance of older stages on natural microhabitats (Fig. 4). While there was a qualitative agreement for *D. aruanus* – most settlers and most older stages occurred inshore – the relative abundance of older life stages offshore (14%) was less than half that expected based on settlement (31%; Fig. 4), a difference that was statistically significant (*P* < 0.05).

Competition between the young of *D. flavicaudus* and *D. aruanus*

In the absence of *D. aruanus*, the population of juvenile *D. flavicaudus* increased by an average of 25% over a 3-month period (Fig. 5). The rate of growth of *D. flavicaudus* populations was not statistically affected by the
presence of the congener (Table 3), although the mean growth rate, while still positive, was reduced by about half (to ~10%) when *D. aruanus* co-occurred on a coral head (Fig. 5). While the difference in the means was not statistically significant, it may be a biologically significant difference that we were unable to discern in our experiment. By contrast, *D. flavicaudus* clearly had a substantial effect on the population growth rate of *D. aruanus*. When alone, juvenile populations of *D. aruanus* grew by more than 50% in 3 months (Fig. 5). However, when *D. flavicaudus* juveniles also were present, the population size of *D. aruanus* declined by nearly 55% in the same period (Fig. 5), a difference that was highly significant (Table 3). This asymmetry between the species in the effect of interspecific competition contrasted with the apparently more reciprocal effect of each species on the other that occurred in the 10-month accumulations (Fig. 3).

**Discussion**

Among the central issues raised by the bipartite life cycle of most marine species are the extent to which spatial patterns of abundance reflect patterns of larval supply, and an understanding of the processes that can obscure such relationships. The results reported here support four main conclusions for a group of ecologically similar damselfishes that have planktonic larvae. First, for both

**Table 2** Two-way analysis of variance tables for the settlement of three species of *Dascyllus* between the inshore and offshore half of lagoons in two different years. The pattern of settlement for each species is presented in Fig. 4.

<table>
<thead>
<tr>
<th>Damselfish species</th>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>D. trimaculatus</em></td>
<td>Between lagoon halves</td>
<td>1</td>
<td>72.0</td>
<td>0.88</td>
<td><em>P &gt; 0.4</em></td>
</tr>
<tr>
<td></td>
<td>Between years</td>
<td>1</td>
<td>112.5</td>
<td>1.38</td>
<td><em>P &gt; 0.3</em></td>
</tr>
<tr>
<td></td>
<td>Lagoon half × year</td>
<td>1</td>
<td>98.0</td>
<td>1.20</td>
<td><em>P &gt; 0.3</em></td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>4</td>
<td>81.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>D. flavicaudus</em></td>
<td>Between lagoon halves</td>
<td>1</td>
<td>3570.1</td>
<td>20.04</td>
<td><em>P &lt; 0.02</em></td>
</tr>
<tr>
<td></td>
<td>Between years</td>
<td>1</td>
<td>66.1</td>
<td>0.37</td>
<td><em>P &gt; 0.5</em></td>
</tr>
<tr>
<td></td>
<td>Lagoon half × year</td>
<td>1</td>
<td>105.1</td>
<td>0.59</td>
<td><em>P &gt; 0.45</em></td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>4</td>
<td>178.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>D. aruanus</em></td>
<td>Between lagoon halves</td>
<td>1</td>
<td>1682.0</td>
<td>6.71</td>
<td><em>P = 0.0606</em></td>
</tr>
<tr>
<td></td>
<td>Between years</td>
<td>1</td>
<td>392.0</td>
<td>1.56</td>
<td><em>P &gt; 0.25</em></td>
</tr>
<tr>
<td></td>
<td>Lagoon half × year</td>
<td>1</td>
<td>32.0</td>
<td>0.13</td>
<td><em>P &gt; 0.7</em></td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>4</td>
<td>250.5</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
spatial scales examined, patterns of settlement into empty microhabitats (a proxy for larval delivery) were neither uniform in space nor similar among the species. Second, there appeared to be relatively high temporal consistency in these spatial patterns of larval delivery (for similar findings for other fishes around Moorea, see Planes et al. 1993; Dufour and Galzin 1993; Dufour et al. 1996). Third, the degree to which spatial patterns of larval delivery were reflected in patterns of relative abundance of older juveniles differed both among the species and between the spatial scales examined. Fourth, the extent of apparent modification of settlement patterns attributable to larval supply was related to the strength of both intra- and interspecific density effects. These patterns were not caused or confounded by spatial differences in the availability of suitable microhabitat as this influence was eliminated by the design of our study. Further, estimates of settlement patterns that were intended to reflect larval supply were not influenced to a great degree by variation in the density of residents on the microhabitats, as these were removed prior to each observed pulse. Finally, the different patterns displayed by the species were not caused by gross differences in the timing of reproduction as the duration of the larval stages of these Dascyllus are similar and settlement of all three species occurred concurrently at Moorea (also see Schmitt and Holbrook in press).

Fig. 4 The relative abundance of settlers (shaded bars) and of older life stages (open bars) on the inshore and offshore halves of lagoons at Moorea. Data are the mean (±1 SE) proportion (per unit suitable habitat) of a life stage of each species on each lagoon half. Statistical analyses of settlement patterns are presented in Table 2.

Fig. 5 The effects of interspecific competition on the population growth of D. flavicaudus and D. aruanus. The figure shows the results of a field experiment where the presence and absence of the congener were manipulated among different coral heads, and the data are the mean (±1 SE) change in population size over 72 days for D. flavicaudus (solid circle) and D. aruanus (open circle). The horizontal dashed line denotes no net change in population size. See Table 3 for ANOVA tables.
bahi anus consistently recruited much more evenly around the island than expected based on larval distributions (Sponaugle and Cowen 1996).

While physical processes that transport dispersing propagules have been recognized as a dominant force structuring benthic marine communities (Sale 1977; Gaines and Roughgarden 1985; Roughgarden et al. 1988; Kingsford 1990; Gaines and Bertness 1992, 1993), there is growing appreciation that larval behavior can modify patterns of delivery and settlement (Keough and Downes 1982; Raimondi 1988, 1991; Leis et al. 1996; Holbrook and Schmitt 1997; Leis and Carson-Ewart 1997). For example, habitat selection by larval fish has been invoked as an explanation for observed mismatches between larval distributions and patterns of early recruitment to the reef environment (Milicich et al. 1992; Doherty et al. 1996; Sponaugle and Cowen 1996). In our system, it is difficult to account for the three qualitatively different patterns of settlement of Dascyllus within the lagoons based on physical transport processes alone. The larvae of these species, which settle concurrently (Schmitt and Holbrook in press), all enter the lagoons over the crest of the barrier reef (Planes et al. 1993; Dufour et al. 1996) yet one species settled uniformly across the lagoon (D. trimaculatus), another settled mostly on the offshore half (D. flavicaudus) and the third settled primarily on the inshore portion (D. aruanus). However, like most studies that have invoked habitat selection by fish larvae, we do not know whether – or if so, how – larval behavior contributes to the observed differences in settlement among the Dascyllus species.

Regardless of the processes that determine spatial patterns of larval delivery, their contribution to shaping patterns of relative abundance of older life stages depends on the extent to which patterns that arise from larval supply are modified by subsequent density dependence (Robertson 1988, 1992; Jones 1991; Schmitt and Holbrook 1996; Steele 1997). If losses of a cohort after settlement are independent of density, then the relationship between spatial patterns of settlement and of older life stages will remain linear (Doherty 1991; Doherty and Fowler 1994). Most studies of reef fish have failed to detect density-dependent loss (see review by Caley et al. 1996), although recent work suggests that density-dependent mortality may be most intense during the first few days after settlement (Schmitt and Holbrook 1999), a period that is seldom investigated in field experiments.

For all three species of Dascyllus at the whole-island scale, the nature of changes in settlement patterns (as estimated from daily counts) were consistent with the operation of density dependence. That is, there were systematic deviations from a linear relationship between the relative abundance of settlers and of older juveniles. These modifications do not appear to be the consequence of a more uniform time-averaged delivery of larvae among these sites, as spatial patterns of settlement (into empty microhabitats) were remarkably consistent among six different cycles spanning 2 years (also see Dufour et al. 1996). Modifications of patterns that arise solely from larval supply can result from density dependence in three different processes: mortality, emigration and settlement. Perhaps one of the most studied is the nature of post-settlement mortality. With respect to these Dascyllus species, detailed analyses of early post-settlement mortality revealed that, regardless of the spatial scale examined, the per capita death rate of each species increased with density of conspecifics, but that mortality was most strongly density-dependent only for a brief period (< 2 weeks) immediately after arrival (Schmitt and Holbrook 1999; also see Schmitt and Holbrook 1996). For the two species that colonized corals (D. flavicaudus and D. aruanus), per capita mortality rates of settlers also increased with density of the other Dascyllus species (Schmitt and Holbrook 1999), indicating that interspecific (as well as intra-specific) competition affected survivorship.

Regarding emigration, the per capita emigration rate of juvenile Dascyllus from the sites also could have increased with density. While very young (small) stages of these species almost never are known to move successfully from the microhabitat to which they settle during at least the first month on the reef (Schmitt and Holbrook 1996, 1999), older, larger juveniles are capable of moving among microhabitats that are separated by several meters. Consequently, we cannot discount the possibility that disproportionately more juveniles moved from sites with higher densities over the 10-month period.

In addition to density dependence in the two sources of loss (death and emigration), the third process where density-dependent modification could have occurred is settlement itself. For a given flux of larvae, settlement of many species of damselfishes is not independent of the density of residents on a microhabitat (Sweatman 1983, 1985; Sweatman and St. John 1990). These priority

Table 3 Analysis of variance tables for the relative change in the sizes of juvenile D. flavicaudus and D. aruanus populations over 72 days in the presence and the absence of the congener. The null hypothesis was that the presence of the congener would have no effect on the population growth rate of the target species. See Fig. 5 for plots of the data

<table>
<thead>
<tr>
<th>Damsel fish species</th>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>D. flavicaudus</td>
<td>Congener presence</td>
<td>1</td>
<td>0.078</td>
<td>0.33</td>
<td>P &gt; 0.5</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>21</td>
<td>0.233</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. aruanus</td>
<td>Congener presence</td>
<td>1</td>
<td>6.254</td>
<td>11.25</td>
<td>P &lt; 0.005</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>21</td>
<td>0.556</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
effects can have a positive or negative effect on settlement. With respect to Dasychilus, Sweatman (1983, 1985) reported that the presence of adult D. aruanus on a coral head resulted in a higher settlement rate than to corals lacking residents. Schmitt and Holbrook (1996) found that low densities of residents also facilitated settlement of D. trimaculatus, but that settlement was inhibited when a microhabitat contained high densities of conspecifics. Similar hump-shaped settler-resident relationships have been found for D. aruanus and D. flavicaudus (R.J. Schmitt and S.J. Holbrook, unpublished work). Thus, over the 10 months when fish accumulated at the experimental sites, the effect of facilitation of settlement at low resident densities and inhibition at higher densities could homogenize abundance among sites even if post-settlement losses were entirely density-independent.

While we do not know the relative contributions of the various density-dependent processes that could have modified the initial settlement patterns, it is quite apparent that the three species differed substantially in the degree to which density dependence altered the initial patterns of settlement. For two species (D. trimaculatus and D. flavicaudus), a signal of settlement was still evident at 10 months (i.e., curvilinear relationships), whereas there was no relationship between settlement pattern and the relative abundance of older D. aruanus juveniles at the whole island scale. The interspecific variation in the strength of density dependence was counter to expectations from the recruitment limitation hypothesis (Doherty 1991). D. trimaculatus consistently had the greatest density of settlers but the least amount of subsequent alteration of the settlement pattern, whereas D. aruanus always had the lowest settlement intensity but the most modification (also see Schmitt and Holbrook 1999). However, Schmitt and Holbrook (1999) found that the per capita mortality rate of young D. aruanus increased the greatest with increasing density, whereas that of D. trimaculatus increased the least with similar increases in density.

The existence and likely the strength of interspecific competition varied systematically among these species. Because D. trimaculatus settled alone to anemones at Moorea, it was subjected only to intraspecific density effects. By contrast, the young of D. aruanus and D. flavicaudus settled into the same coral heads, and the relatively greater modification of settlement patterns for these species could have been due to the added component of interspecific competition. This hypothesis was supported by our findings. The observation that D. aruanus was affected to a much greater extent by D. flavicaudus than vice versa could help explain why the settlement pattern of D. aruanus was modified the most at both scales examined. Overall, these findings highlight the need to further investigate the particular mechanisms that produce interspecific variation in larval delivery and the contributions of various processes that are responsible for density-dependent modification of settlement patterns.

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