Oecologia (1998) 115:268–277

Laura Gutiérrez

Habitat selection by recruits establishes local patterns of adult distribution in two species of damselfishes: *Stegastes dorsopunicans* and *S. planifrons*

Received: 27 May 1997 / Accepted: 4 January 1998

Abstract Local patterns of adult distribution in organisms that disperse young as pelagic larvae can be determined at the time of recruitment through habitat selection or, shortly thereafter, through post-recruitment processes such as differential juvenile survivorship and interspecific competition. This study addresses the importance of habitat selection by recruits in establishing the local pattern of adult distribution in two sympatric Caribbean damselfish species, *Stegastes dorsopunicans* and *S. planifrons*. Both species inhabit shallow reefs but show little overlap in their distribution; *S. dorsopunicans* predominates in the reef crest and *S. planifrons* occurs primarily on the reef slope. Furthermore*,* *S. dorsopunicans* is associated with rocky substrate, while *S. planifrons* occupies live coral. The substrate cover follows a similar pattern with coral being much less common on the reef crest than on the reef slope. Monitoring recruitment every other day in reciprocal removal experiments and artificial reefs indicates that the observed pattern of local adult distribution is a product of habitat selection for both species. The presence or absence of conspecifics did not influence recruitment patterns for either species. *Stegastes dorsopunicans* recruited primarily to shallow, rocky areas, appearing to cue on both substratum type and depth. *Stegastes planifrons* recruited exclusively to coral substratum independent of depth. These results indicate that local adult patterns of distribution can be explained by habitat selection at recruitment, and that substrate type and depth may be important cues.

Key words Habitat selection · Distribution · Damselfish · Recruitment · Coral-reef fishes

Introduction

The population dynamics of species with open populations, such as many nearshore marine organisms which possess a planktonic larval stage, has received much attention over the last decade (Roughgarden et al. 1985, 1988; Victor 1986; Underwood and Fairweather 1989; Gaines 1992). Variable recruitment can influence the patterns and processes of local community structure. For example, an abundant supply of larvae can increase population density and consequently the intensity of biological interactions (e.g., competition and predation) within the community, whereas a limited supply of larvae may have the opposite effect (Pacala and Silander 1985; Roughgarden et al. 1988; Pacala 1989). Thus, local patterns of adult distribution in marine organisms which disperse primarily during a larval stage will be established either at settlement through habitat selection, or thereafter through processes such as differential predation, competition, and/or habitat selection through migration (Raimondi 1991).

It is important to distinguish between settlement and recruitment since these two events give complementary, but different insights into the processes structuring communities. Settlement is the initial establishment of larvae onto the substratum. Recruitment, on the other hand, is the first record of the settled larvae (*sensu* Keough and Downes 1982). While a settler's age is zero, the age of a recruit can vary from hours (Raimondi 1991) to months (Doherty and Fowler 1994). A pattern of distribution and abundance described at settlement reflects only larval processes; if it is described at recruitment, it also includes the effects of post-settlement processes.

As in many marine organisms, the life cycle of most coral reef fishes involves a dispersive planktonic larval phase (Sale 1980). Hence, abundance and distribution patterns of fishes on the reef can be determined by both settlement and post-settlement processes. Much attention has been given to post-settlement processes. In the

---

L. Gutiérrez
Department of Biology, University of Houston,
Houston, TX 77204-5513, USA
Fax: (713)743-2636; e-mail: Lgutierrez@uh.edu

past, competition was considered to be the major process structuring fish communities (references in Sale 1980). Predation has received attention more recently (Hixon 1991). The focus on recruitment has been directed primarily to its role in regulating the abundance of fish populations (Doherty and Williams 1988; Doherty 1991). Little attention has been paid to its function in the establishment of local patterns of distribution; for example, through habitat selection.

Habitat selection, the active choice of a living site by an individual, may limit the distribution of species yet allow potentially competing individuals or species to coexist. Habitat selection may occur at settlement or anytime thereafter. Because recruitment patterns provide a static snapshot of a perhaps dynamic process, they can be used to study habitat selection at settlement, provided recruitment is censused frequently.

Many coral reef fishes disperse only during the planktonic phase assuming a sedentary, sometimes territorial existence soon after settlement. Numerous studies on coral reef fish have revealed the importance of habitat characteristics to fish survivorship and growth, for example, different reefs (Aldenhoven 1986), depths (Jones 1986; Shapiro 1987; Wellington 1992), densities (Jones 1987; Forrester 1995; Hixon and Beets 1993) and substrata (Jones 1988; Booth 1992; Wellington 1992). These results indicate that there should be strong selective pressure for fish to choose the proper habitat at, or soon after, settlement. In fact, many studies have shown habitat selection in reef fishes (Shulman et al. 1983; Sweatman 1983; Holbrook and Schmitt 1988; Carr 1991; Levin 1991; Booth 1992; Wellington 1992; Danilowicz 1996). Some fish species have been shown to cue on habitat complexity (Carr 1991; Levin 1991), as well as on abundance of predators (Shulman et al. 1983), conspecifics and congeners (Sweatman 1985, 1988; Booth 1992), or specific substrata (Sale 1971; Marliave 1977; Danilowicz 1996). Few studies, however, have attempted to relate habitat selection to community structure (Wellington 1992). Habitat selection at, or soon after, settlement may determine local adult patterns of distribution. Wellington (1992) showed that *Stegastes leucostictus* and *S. variabilis* settlement was confined to conspecific adult habitats.

In the present study, I monitored early recruitment of *S. dorsopunicans* (Poey) and *S. planifrons* (Cuvier) to assess whether or not recruits select their habitat based on conspecifics, congeners, substratum and depth. I specifically addressed the importance of recruitment processes in establishing local patterns of adult distribution.

Methods

Study species

Damselfishes (Pomacentridae) represent one of the largest families of fishes inhabiting tropical reefs, and are numerically and functionally important members of coral reef fish communities. Damselfishes of the genus *Stegastes* are relatively small territorial fish (Itzkowitz 1977; Robertson et al. 1981, Robertson 1984). These territories are utilized for food, shelter, and nesting (Thresher 1976). Most adult damselfishes grow a dense algal mat within their territories from which they feed. They control the species composition of these algal turfs, and defend them against other herbivores such as fish and sea urchins (Myrberg and Thresher 1974; Thresher 1976). In order to provide substratum for this algal mat, some adult damselfishes may kill live coral within their territories, thus, affecting the benthic algal and coral communities (Brawley and Adey 1977; Kaufman 1977; Lobel 1980; Williams 1980; Robertson *et al.* 1981; Wellington 1982; Hixon and Brostoff 1983; Foster 1987; Knowlton *et al.* 1990). Their territories also serve as shelter, containing holes or crevices where the fish hide from predators. These shelters are defended against other diurnal fishes (Robertson and Sheldon 1979). Finally, all damselfishes lay benthic eggs. Females deposit eggs inside the male territory, and males aerate the nest and defend it against piscivores until hatching (Thresher 1984).

Several studies have shown habitat partitioning among damselfish species (Itzkowitz 1977; Williams 1978; Waldner and Robertson 1980; Robertson 1984; Wellington 1992). Six species of the genus *Stegastes* occur on Caribbean reefs: *S. diencaeus*, *S. dorsopunicans*, *S. leucostictus*, *S. partitus*, *S. planifrons*, and *S. variabilis*. The two species chosen for this study (three-spot damselfish, *S. planifrons*, and dusky damselfish, *S. dorsopunicans*) are common throughout the Caribbean and easily distinguishable on the basis of their coloration both as juveniles and adults. The depth range of *S. planifrons* is broader including both shallow and deep reefs, and *S. dorsopunicans* inhabits shallow reefs (0.5–5 m). Even on shallow reefs, however, these two species show little overlap in their distribution (Waldner and Robertson 1980; Robertson 1984). The extent of the overlap seems to be related to the steepness of the transition between the reef crest and the reef slope (personal observation). Thus, these two damselfishes provide an ideal system to examine the recruitment and post-recruitment processes establishing local adult distributions.

Study site

The study was carried out at the Smithsonian Tropical Research Institute field station in the San Blas Comarca, Panama. Shallow reefs in this area are dominated by *Millepora complanata* on the crest and *Agaricia* spp. on the slope, with *Porites porites*, *P. furcata*, *P. astreoides* and *Montastraea* spp. also being common.

The study area was composed of four shallow (0.5–5 m) patch reefs at Punta de San Blas (Fig. 1) differing in coral cover, wave action, etc. These reefs are separated from each other by 100–400 m of sand which minimizes the possibility of fish migration between reefs. Thus, individual reefs were considered independent replicates. *Stegastes planifrons* and *S. dorsopunicans* are the most common damselfishes on these reefs. The other relatively common damselfish is *Microspathodon chrysurus* which is larger than both *Stegastes* species and occupies shallow *Millepora* colonies. Its territories are superimposed on *Stegastes* territories (Robertson 1984). *Microspathodon chrysurus* seems to use its size-based dominance to preempt food from its cohabitants; and in doing so, reduces the growth rate of *S. dorsopunicans* but does not appear to affect their distribution patterns (Robertson 1984).

Patterns of adult abundance and distribution

To determine the patterns of adult abundance and distribution in the study area, four 1-m-wide transects were run from the center to the edge of each reef (6–11.4 m). I recorded depth and substratum every 10 cm, as well as the extent of the reef crest and the reef slope. All fish found defending territories within 0.5 m on either side of the transect were counted. These numbers were converted to densities (individuals/m^2) using the area covered by each transect.

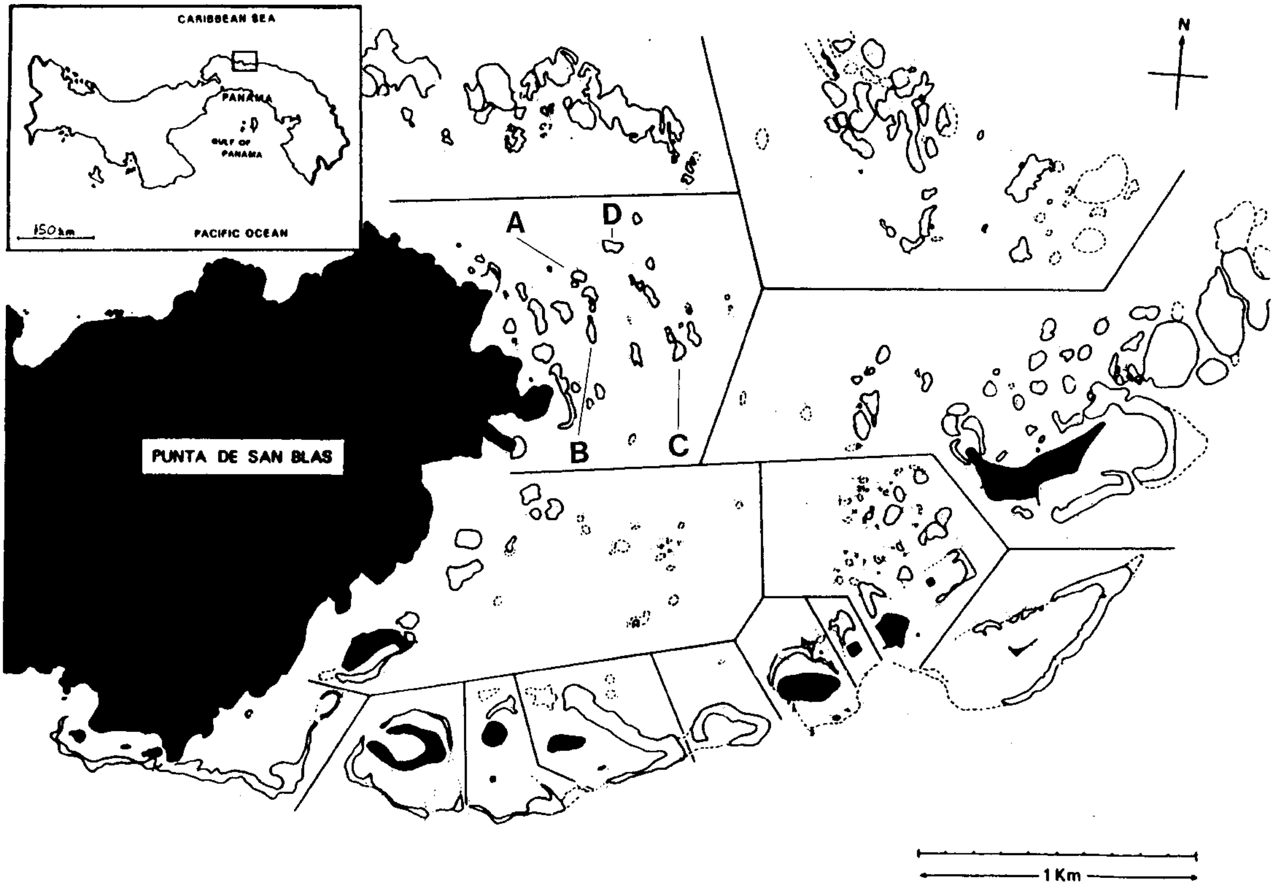

Fig. 1 Partial map of the San Blas Comarca showing the location of the four study reefs (**A**, **B**, **C**, and **D**). Punta de San Blas is the northern end of the Comarca. The current runs along a north-south direction during most of the year with a few days during the summer months (July-August) running in the opposite direction

Habitat selection and local patterns of distribution

To test the null hypothesis that there is no habitat selection at recruitment, three treatments were applied to each reef: a control and two reciprocal removal treatments (SDR, *S. dorsopunicans* removal and SPR, *S. planifrons* removal). Each treatment occupied a 50-m^2 area on the reef and was separated from the next treatment by at least 7 m. Each 50-m^2 area was divided equally into two zones: the reef crest and the reef slope. Furthermore, I categorized available substrata within these zones as either coral (living colonies) or rock (dead corals). Prior to the collection of recruitment data, I removed fish using microspears and quinaldine anaesthetic. Because conspecifics from immediate adjacent areas tend to invade vacated territories (e.g., Waldner and Robertson 1980), subsequent removals were necessary to maintain the treatments. Immigrants were removed at least once a month with an overall removal efficiency of 85–90% (Fig. 2).

I monitored recruitment over the entire 50-m^2 area for each treatment every other day for 5 months. To facilitate the sampling, I further divided the areas into 1.5-m^2 quadrats. The location of recruits, along with their associated substratum, were recorded.

Cues to habitat selection

Differences in recruitment among treatments (presence or absence of conspecifics or potential competitors), between zones (crest or slope), and between substrata (coral or rock) were used to identify potential settlement cues. The role of priority effects (i.e., the effect of conspecific/congener presence on habitat selection) was investigated by following recruitment into removal sites. Depth and substratum-specific cues were examined by comparing recruitment along a depth gradient and in different types of substrata, respectively.

Finally, to separate substratum- from depth-effects, two small (3–5 m^2) artificial reefs were established on each experimental reef, outside the study areas: one on the reef crest, at about 1 m depth (shallow treatment) and the other 2 m from the reef edge, at about 4 m depth (deep treatment). Rocks and living coral (*Agaricia* spp. and *Millepora* spp.) were used to build the artificial reefs. The area covered by each type of substratum was calculated (approximately 70–80% rock and 20–30% coral). Surveys for recruits were made every other day for 1.5 months. All recruits found were removed with the use of anaesthetic (quinaldine) and hand nets after making a note of the substratum they were found in.

Statistical analyses

For each area (treatment) within a reef, I estimated the proportion of coral and rock in each of the 1.5-m^2 quadrats. These estimates were then added and the total cover (in m^2) of coral and rock for each zone on the reef was calculated (Table 1).

For the statistical analyses, the numbers of recruits were converted to numbers per unit area of substratum. Recruit densities were analyzed with a mixed factorial ANOVA, where reefs constitute the replication factor (random), and treatment, zone and substratum are fixed factors (Wilkinson 1991). The substratum factor was excluded from the *S. planifrons* analysis since all individuals recruited to a single substratum type. Each removal treatment was also tested individually against the control to partition the effects of presence or absence of conspecifics and congeners on recruitment. *Stegastes dorsopunicans* recruitment densities

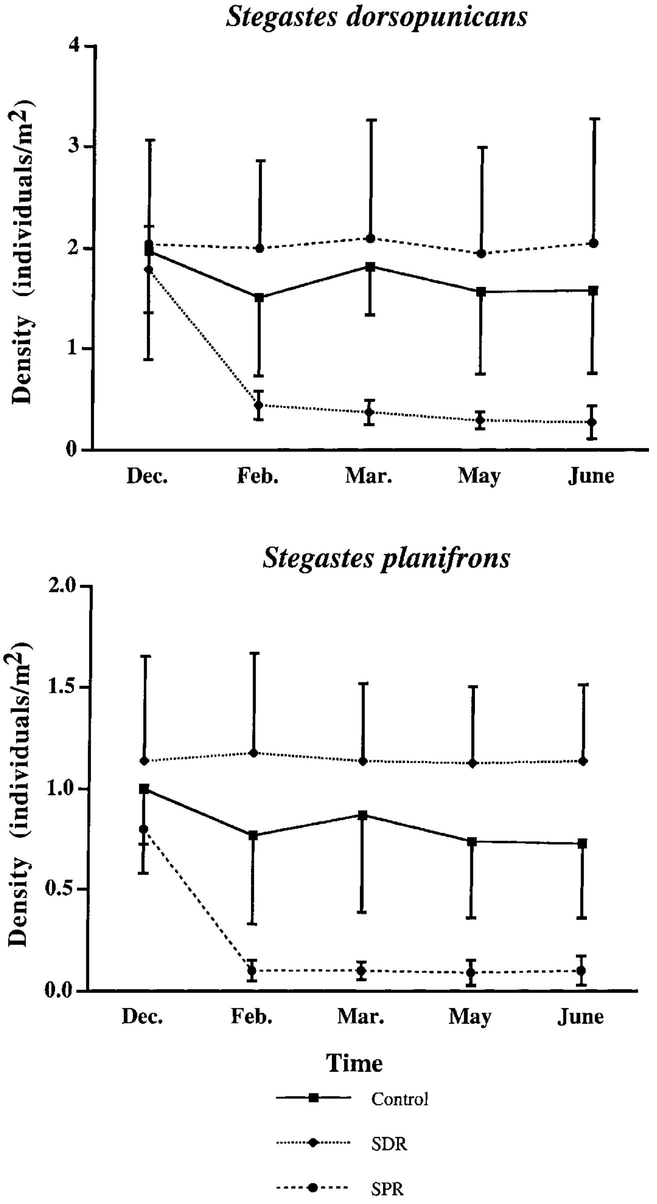

Fig. 2 Efficiency of adult removals in experimental areas. Density of adults (individuals/m^2) over time in the three treatments: Control, *Stegastes dorsopunicans* removal (*SDR*), and *S. planifrons* removal (*SPR*). Densities were estimated approximately halfway between removals. *Bars* represent SEs ($n = 4$)

were also tested with a mixed factorial ANCOVA using percentage cover of substratum as a covariate. This was done to control for the natural variation in substratum cover among treatments and zones. In the artificial reefs experiment, the numbers of recruits were also converted to numbers per unit area of substratum and analyzed using a Student's *t*-test (Wilkinson 1991).

The statistical power of the different tests was assessed by calculating the standard deviation of the standardized population means (f). Tables were used to obtain the power of the dependent factors and interactions resulting from a three way analysis of variance (Cohen 1969). For the t-test, power was derived using SigmaStat (Jandel 1994).

Results

Patterns of adult abundance and distribution

Results from the 1-m-wide transects show that adult *S. dorsopunicans* inhabit the reef crest while adult *S. planifrons* occupy the reef edge and slope (Fig. 3). At the interface between the reef crest and slope the distribution of these two species overlaps and they are found at comparable densities (0.6 individuals/m^2). Although a few individuals reside in the opposite reef zone, these represent less than 20% of the preferred-zone densities (Fig. 3). Besides occupying different reef zones, these species seem to be identified with unlike substrata, for example adults of *S. dorsopunicans* preferentially occupy rock, whereas *S. planifrons* inhabit living coral.

Habitat selection and local patterns of distribution

Neither *S. dorsopunicans* nor *S. planifrons* showed random patterns of recruitment in control plots. Each species recruited in significantly higher densities to the zones of the reef typically inhabited by their conspecifics (Table 2). Recruits of *S. dorsopunicans* dominated the reef crest, whereas recruits of *S. planifrons* were most abundant on the reef slope (Fig. 3).

Cues to habitat selection

Recruit densities did not differ significantly among the three treatments in either species (Fig. 4). While *S. planifrons* recruit densities were 15% lower in the SPR than in the control treatment, those of *S. dorsopunicans* were only 3% lower in the SDR than in the control treatment. Moreover, the pattern observed between reef zones in the controls versus the removal treatments did not differ (Fig. 5). Recruitment to the two substrata, however, was significantly different for both species. While recruits of *S. dorsopunicans* preferred rock over coral, *S. planifrons* recruited exclusively to coral (Fig. 6).

Results from the mixed factorial ANOVA for *S. planifrons* showed the treatment effect to be non-significant while the zone effect was highly significant (Table 2). The power for the treatment, however, was very low (25%) indicating that the probability of detecting a real effect of conspecifics was low. The analyses of variance testing for differences between the control and removals (SPR and SDR) independently gave the same results: non-significant treatment effects and significant zone effect. The power for the treatment was again low (23%).

The results for *S. dorsopunicans* are similar. The mixed factorial ANOVA indicates non-significant treatment effect and significant zone, substratum, and zone × substratum interaction effects (Table 2). An analysis of covariance controlled for the effects of nat-

Table 1 Total substratum cover in all four reefs divided by reef zone and treatment (m^2). I estimated the proportions of each substratum (e.g., *Agaricia*, *Millepora*, rock, sponge, algae) in each 1.5-m^2 quadrat. These proportions were converted to areas (m^2) and summed over each zone to obtain the total cover. All the coral species were added to produce a single estimate of coral. The last two columns separate coral cover into *Agaricia* spp. and the other coral species. Values are added across treatments within a reef. (Treatments: *CON* control, *SDR Stegastes dorsopunicans* removal, *SPR S. planifrons* removal)

Reef[a]	Reef zone	Substratum							
		Coral			Rock			*Agaricia*	Other
		CON	SDR	SPR	CON	SDR	SPR		
A	Crest	9.94	13.50	12.25	14.42	15.24	15.61	13.70	21.99
	Slope	9.39	12.26	14.79	10.15	10.57	4.74	18.67	17.77
B	Crest	18.34	2.27	12.28	12.74	20.40	14.19	5.58	27.31
	Slope	13.18	13.24	16.68	2.39	1.54	7.07	37.16	15.94
C	Crest	6.95	10.40	9.98	21.61	12.70	13.36	9.43	17.90
	Slope	12.31	12.15	16.39	1.55	8.33	5.27	24.18	16.67
D	Crest	22.54	18.70	19.05	8.54	9.20	6.83	16.90	43.39
	Slope	14.38	12.97	12.20	0.62	5.15	12.05	21.97	17.58

[a] See Fig. 1

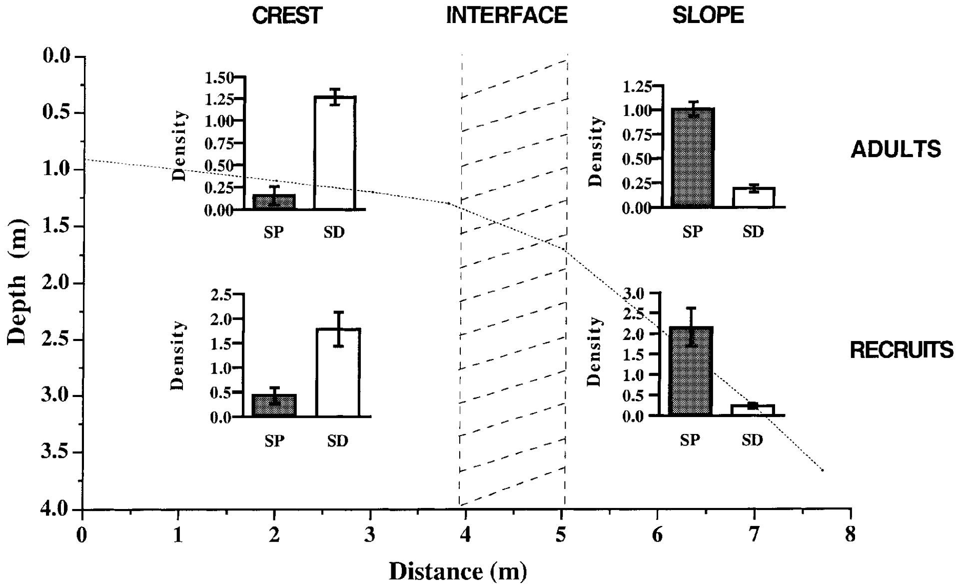

Fig. 3 Typical profile of study reefs beginning at the middle of the reef crest (0 m) to the sand edge. *Shaded area* depicts the interface between the two zones (crest and slope). *Bar graphs* illustrate the distribution of adults and recruits in the two reef zones. Adult densities were obtained from four 1-m-wide transects run vertically along each experimental reef. All fish found within 1 m of a transect line were counted and density subsequently calculated based on transect length (6–11.4 m). Both species were found in equal densities in the interface zone (~0.6 fish/m^2). Recruit densities were obtained by documenting recruitment every other day during five months in the control plots, and dividing the number of recruits by the area. (*SD Stegastes dorsopunicans*, *SP S. planifrons*). *Error bars* represent SEs ($n = 4$)

ural variation in substratum cover. Although the assumption of homogeneity of slopes was not met, the test was run since these discrepancies are thought to have a conservative effect (i.e., smaller type I error) on the ANCOVA *F*-test (Huitema 1980). The ANCOVA results agree with the ANOVA in showing non-significant treatment effects and significant zone effects; however, the substratum covariate was not significant.

In the artificial reefs experiment, *S. dorsopunicans* recruited exclusively to rocky substratum and *S. planifrons* to coral colonies. Even though *S. planifrons* recruited preferentially to deep rather than to shallow areas, the difference was non-significant ($P = 0.550$). The power of the test in this comparison, however, was quite low (5%). *Stegastes dorsopunicans* recruited significantly more to the shallow areas ($P = 0.014$) (Fig. 7).

Discussion

Habitat selection and local patterns of distribution

There are numerous studies dealing with the importance of recruitment processes in determining abundances of adult populations in marine organisms (e.g., Sale 1977; Findley and Findley 1985; Gaines et al.

Table 2 Results of mixed factorial analyses of variance for the effects of treatment (control, *S. dorsopunicans* removal, and *S. planifrons* removal), zone (crest and slope), and substratum (coral and rock) on recruitment of *S. dorsopunicans* and *S. planifrons* ($n = 4$)

Source	*df*	SS	*F* ratio	*P*	β
A *S. dorsopunicans*					
Reef	3	1.096	0.625	0.625	
Treatment	2	0.611	0.676	0.544	0.75
Zone	1	28.872	515.57	0.000	
Substratum	1	28.751	103.794	0.002	
Treatment × Zone	2	0.338	0.210	0.816	0.93
Treatment × Substratum	2	1.225	2.063	0.208	0.25
Zone × Substratum	1	19.098	116.450	0.002	
Treatment × Zone × Substratum	2	0.991	0.847	0.474	
B *S. planifrons*					
Reef	3	4.256	0.264	0.850	
Treatment	2	1.350	0.858	0.470	0.75
Zone	1	35.062	71.119	0.003	
Treatment × Zone	2	0.534	0.170	0.848	0.94

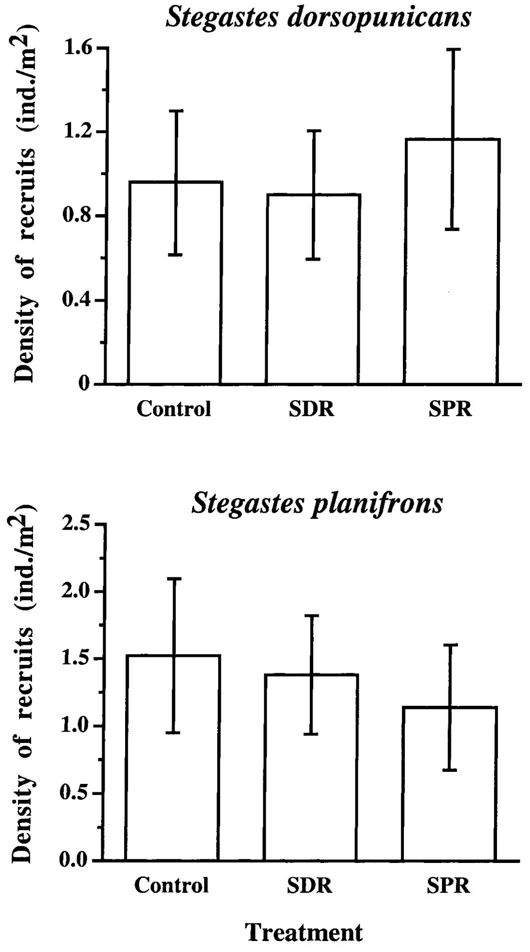

Fig. 4 Mean densities of *S. dorsopunicans* and *S. planifrons* recruits in controls, SDR, and SPR treatments. Recruit densities were based on number of recruits over 5 months of sampling. *Bars* represent SEs. Treatments did not differ significantly for either species ($P > 0.4$) ($n = 4$)

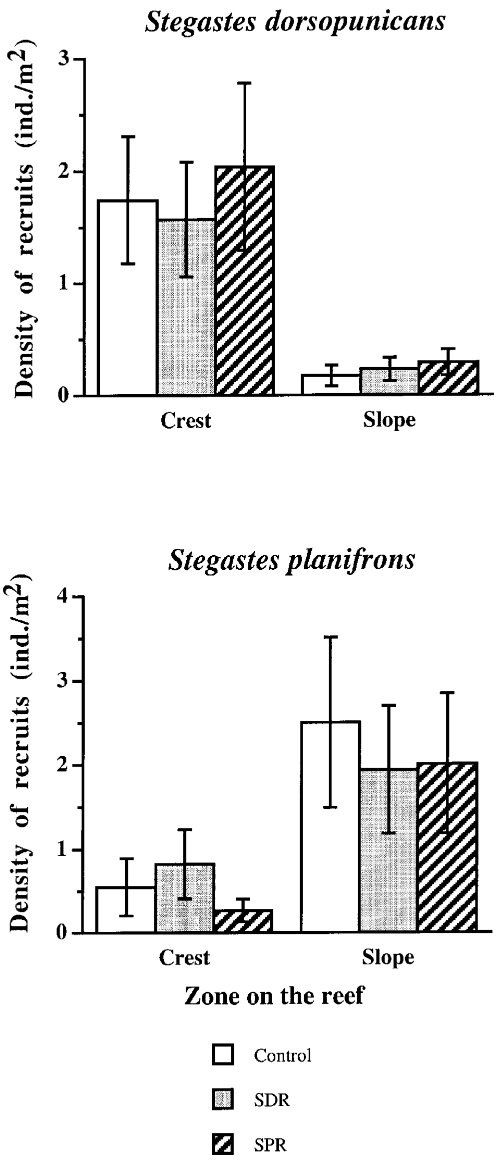

Fig. 5 Mean densities of *S. dorsopunicans* and *S. planifrons* recruits on the reef crest (shallow) and reef slope (deep) by treatment. Recruit densities were based on number of recruits over 5 months of sampling. *Bars* represent SEs. Recruitment to the reef zones differed significantly in both species ($P < 0.001$) ($n = 4$)

1985; Victor 1986; Doherty and Williams 1988; Roughgarden et al. 1988; Underwood and Fairweather 1989; Jones 1990; Stoner 1990; Olafsson et al. 1994). In contrast, little attention has been paid to the importance of recruit behavior as a mechanism determining local adult distributions (Connell 1985; Butman 1987; Raimondi 1991; Wellington 1992). Local distributions have been related more to post-recruitment processes such as predation, migration, and competition (Williams 1991).

I found that both *S. dorsopunicans* and *S. planifrons* display non-random recruitment patterns (Fig. 3). Both species recruit in higher numbers to the adult habitat, thereby establishing the local patterns of distribution

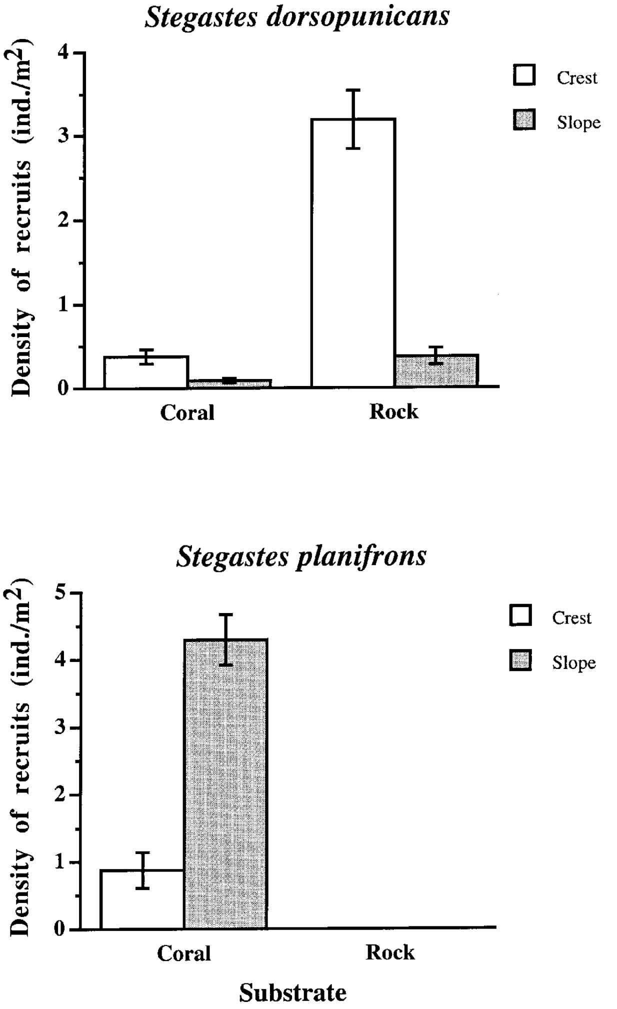

Fig. 6 Mean densities of *S. dorsopunicans* and *S. planifrons* recruits in the two substrata (coral-living and rock-dead) by reef zone. Recruit densities were based on number of recruits over 5 months of sampling. *Bars* represent standard errors. Both species showed highly significant substratum preferences ($P < 0.001$) ($n = 4$)

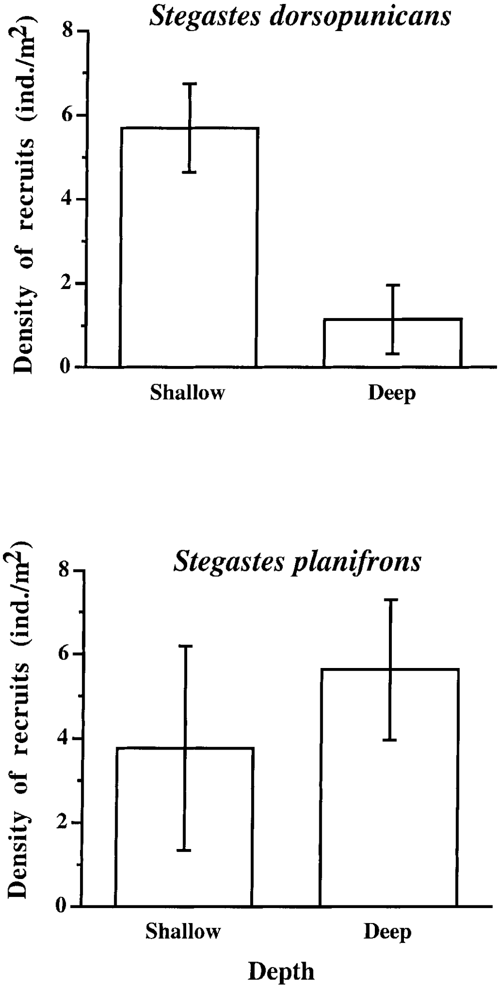

Fig. 7 Mean densities of *S. dorsopunicans* and *S. planifrons* recruits in the shallow (reef crest) and deep (reef edge) artificial reefs. Recruitment was documented every other day for 1.5 months. *S. dorsopunicans* recruited exclusively to rocks and significantly more to shallow areas (*t*-test, $P < 0.05$). *S. planifrons* recruited solely to coral at both depths (*t*-test, $P > 0.5$). *Bars* represent SEs ($n = 4$)

observed for adult conspecifics on the reef. Similarly, Wellington (1992) observed that the distribution of two other congeners, *S. leucostictus* and *S. variabilis*, in St. Croix (United States Virgin Islands) was established by recruits. Habitat selection may be a common process structuring coral reef fish communities (Sale 1971; Sweatman 1983, 1985, 1988; Sale et al. 1984; Booth 1992; Tolimieri 1995; Danilowicz 1996) and may account for the habitat partitioning observed in some coral reef fishes (e.g., Itzkowitz 1977; Robertson and Lassig 1980; Waldner and Robertson 1980; Anderson et al. 1981; Findley and Findley 1985).

Cues to habitat selection

Even if larvae have evolved the ability to select where they settle, what proximate cues allow them to find the right habitat? The literature regarding metamorphosis and settlement cues ranges from ecological studies looking at habitat complexity (Carr 1991; Levin 1991), different substrata (Marliave 1977; Sale et al. 1984; Victor 1986; Danilowicz 1996), and species interactions (Sweatman 1985, 1988), to chemical studies striving to identify the precise molecules involved in the process (Murata et al. 1986; Morse 1990; Pawlik 1992; Rodriguez et al. 1993).

In this study, *S. planifrons* showed a strong substratum preference by recruiting exclusively to living coral, independent of depth (Fig. 6). The significant zone factor, however, indicates that substratum and zone may have a joint effect, such that, substratum specific cues cannot be separated from depth effects. This result might seem surprising given the little difference found in coral cover between zones (Table 1). However, coral substratum combines all species of coral into one category when, in reality, most *S. planifrons* (93%) recruited to *Agaricia* spp. which is more common on the reef slope

(Table 1). *Millepora* spp. and *Porites* spp. are the other major coral taxa and account for the majority of coral substratum found on the reef crest (Table 1). The fact that 93% of *S. planifrons* recruited to *Agaricia* spp., together with the non-significant results from the artificial reef experiment indicate that depth alone may play only a minor role in this species' habitat selection (Table 2, Fig. 7). Although *S. planifrons* recruits in larger numbers to the deeper zone, it may be simply selecting for the more abundant preferred live coral habitat (Table 1). *Stegastes dorsopunicans*, on the other hand, seems to be cueing more strongly on depth than substratum. While *S. dorsopunicans* prefers rocky substratum, it recruited significantly more to shallow areas in the artificial reefs experiment, even though the appropriate substratum was available at both depths. Also, results of the analysis of covariance indicated that the covariate (substratum) was not significant. If true, the observed significant zone × substratum interaction can be interpreted as an artifact of higher recruitment to shallower areas: on the reef crest (shallow), *S. dorsopunicans* recruits in large numbers preferentially to rocky substratum while, on the slope (deep), recruitment levels are so low that differences between substrata could not be detected (Table 2, Fig. 6).

It is possible that larvae may cue on something other than substratum. Both Sweatman (1985) and Booth (1992) showed that larvae responded to residents' cues by settling preferentially with conspecifics and/or *congeners*. Settling near conspecifics can clearly be advantageous in locating both appropriate substratum and mates for reproduction. At the same time, however, there may be negative effects on growth and survival due to intra- and/or interspecific competition. Jones (1987) found that growth and maturation time were inversely related to the density of conspecifics (juveniles and adults at different time periods). Schmitt and Holbrook (1996), on the other hand, found no effect on juvenile survivorship at low conspecific densities, but a negative effect at higher densities. Therefore, the role of conspecifics as recruitment cues may be species-specific. The role of conspecifics in affecting recruitment was addressed here by examining recruitment in the absence of both adults and juveniles. While the results of the statistical tests were nonsignificant, the power to detect differences was also very low (Table 2). Nonetheless, there was a clear trend of fewer *S. planifrons* recruits in the absence of conspecifics than there was for *S. dorsopunicans* (Fig. 4). Even though cueing on established conspecifics might be advantageous as outlined above, it might not be so if the species exhibit ontogenetic shifts in habitat use. In Honduras, Lirman (1994) found that juveniles and adults of *S. planifrons* have non-overlapping distributions. Although not the case in San Blas, Lirman's observation might indicate cueing on absence of conspecifics if non-overlapping distributions are common in other places.

Fish are thought to settle at night to avoid predators (Victor 1986; Booth 1991) and so it has been postulated that they may rely on olfactory rather than visual cues to locate appropriate habitat (Murata et al. 1986; Sweatman 1988; Danilowicz 1996; Elliot et al. 1995). Settlement, however, may be a passive process, a result of potential spatial differences in larval supply. It is possible that fish settle randomly and subsequently migrate and/or incur differential mortality. To distinguish between habitat selection by settlers versus recruits, one needs to observe the actual process of settlement. Recruitment in this study was observed soon after settlement (5–48 h) and recruits were never observed to move far from their original location. Even if settlers migrated immediately after arriving on to the reef, this would still fit the definition of habitat selection at recruitment since it would imply that recruits are actively seeking the appropriate microhabitat. On the other hand, if the observed patterns result from differential survivorship, this definition would fail since neither settlers nor recruits would play an active role in the establishment of local adult distribution patterns. However, differential mortality would have to be extremely common and occur at very high rates to alter the settlement patterns over such a short period of time.

In this study, both species appear to establish local adult patterns of distribution during early recruitment. However, these species use different cues and the selective forces operating on the evolution of habitat selection may also vary between them. It appears, however, that substratum and depth are more important than presence of conspecifics. Therefore, it is plausible that habitat-specific requirements may ultimately drive the evolution of habitat selection in this system.

Acknowledgements Thanks are extended to the Kuna indians of the Comarca of San Blas and the Government of the Republic of Panama for permitting field work in San Blas. I thank G. Etchelecu, F. Gutiérrez, M. Meekan, L. Rogers, M. Seidman, M. Soriano, and R. Tapia for their assistance in the field. A.P. Klimley, B. Victor, G. Wellington, D. Wiernasz, T. Wilcox, and an anonymous reviewer provided helpful comments on the manuscript. This study was supported by a Smithsonian Tropical Research Institute Shor-Term Fellowship, and by a Department of Biology Research Fellowship and Coastal Center Grant from the University of Houston.

References

Aldenhoven JM (1986) Local variation in mortality rates and life-expectancy estimates of the coral reef fish *Centropyge bicolor* (Pisces: Pomacanthidae). Mar Biol 92:237–244

Anderson GRV, Ehrlich AH, Ehrlich PR, Roughgarden JD, Russell BC, Talbot FH (1981) The community structure of coral reef fishes. Am Nat 117:476–495

Booth DJ (1991) The effect of sampling frequency on estimates of recruitment of the domino damselfish *Dascyllus albisella* Gill. J Exp Mar Biol Ecol 145:149–159

Booth DJ (1992) Larval settlement and preferences by domino damselfish *Dascyllus albisella* Gill. J Exp Mar Biol Ecol 155:85–104

Brawley SH, Adey WH (1977) Territorial behavior of threespot damselfish (*Eupomacentrus planifrons*) increases reef algal biomass and productivity. Environ Biol Fish 2:45–51

Butman CA (1987) Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. Oceanogr Mar Biol 25:113–165

Carr MH (1991) Habitat selection and recruitment of an assemblage of temperate zone reef fishes. J Exp Mar Biol Ecol 146:113–137

Cohen J (1969) Statistical power analysis for the behavioral sciences. Academic Press, New York

Connell JH (1985) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. J Exp Mar Biol Ecol 93:11–45

Danilowicz BS (1996) Choice of coral species by naive and field-caught damselfish. Copeia 1996:735–739

Doherty PJ (1991) Spatial and temporal patterns in recruitment. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, pp. 261–293

Doherty PJ, Fowler AJ (1994) An empirical test of recruitment limitation in a coral reef fish. Science 263:935–939

Doherty PJ, Williams DM (1988) The replenishment of coral reef fish populations. Oceanogr Mar Biol 26:487–551

Elliot JK, Elliot JM, Mariscal RN (1995) Host selection, location, and association behaviors of anemonefishes in field settlement experiments. Mar Biol 122:377–389

Findley JS, Findley MT (1985) A search for pattern in butterfly fish communities. Am Nat 126:800–816

Forrester GE (1995) Strong density-dependent survival and recruitment regulate the abundance of a coral reef fish. Oecologia 103:275–282

Foster SA (1987) Territoriality of the dusky damselfish: influence on algal biomass and on the relative impacts of grazing by fishes and Diadema. Oikos 50:153–160

Gaines SD (1992) Dispersal of juveniles and variable recruitment in sessile marine species. Nature 360:579–581

Gaines S, Brown S, Roughgarden J (1985) Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. Oecologia 67:267–272

Hixon MA (1991) Predation as a process structuring coral reef fish communities. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, San Diego pp 475–508

Hixon MA, Beets JP (1993) Predation, prey refuges, and the structure of coral reef fish assemblages. Ecol Monogr 63:77–101

Hixon MA, Brostoff WN (1983) Damselfish as keystone species in reverse: intermediate disturbance and diversity of reef algae. Science 220:511–513

Holbrook SJ, Schmitt RJ (1988) The combined effects of predation risk and food reward on patch selection. Ecology 69:125–134

Huitema BE (1980) The analysis of covariance and alternatives. Wiley, New York

Itzkowitz M (1977) Spatial organization of the Jamaican damselfish community. J Exp Mar Biol Ecol 28:217–241

Jandel (1994) SigmaStat. Jandel Scientific, San Rafael, CA

Jones GP (1986) Food availability affects growth in a coral reef fish. Oecologia 70:136–139

Jones GP (1987) Some interactions between residents and recruits in two coral reef fishes. J Exp Mar Biol Ecol 114:169–182

Jones GP (1988) Experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of two coral reef fishes. J Exp Mar Biol Ecol 123:115–126

Jones GP (1990) The importance of recruitment to the dynamics of a coral reef fish population. Ecology 71:1691–1698

Kaufman L (1977) The threespot damselfish: effects on benthic biota of Caribbean coral reefs. In: Taylan DL (ed) Proceedings of the 3rd International coral reef symposium. Vol. 1 The School, Miami, pp. 559–564

Keough MJ, Downes BJ (1982) Recruitment of marine invertebrates: the role of active larval choices and early mortality. Oecologia 54:348–352

Knowlton N, Lang JC, Keller BD (1990) Fates of staghorn coral isolates on hurricane-damaged reefs in Jamaica: the role of predators. In: Choat SH (ed) Proceedings of the 6th international coral reef symposium. Vol. 2 Symposium Executive Committee, Townsville, Australia. pp. 83–88

Levin PS (1991) Effects of microhabitat on recruitment variation in a Gulf of Maine reef fish. Mar Ecol Prog Ser 75:183–189

Lirman D (1994) Ontogenetic shifts in habitat preferences in the three-spot damselfish, *Stegastes planifrons* (Cuvier), in Roatan Island, Honduras. J Exp Mar Biol Ecol 180:71–81

Lobel PS (1980) Herbivory by damselfishes and their role in coral reef community ecology. Bull Mar Sci 30:273–289

Marliave JB (1977) Substratum preferences of settling larvae of marine fishes reared in the laboratory. J Exp Mar Biol Ecol 27:47–60

Morse DE (1990) Recent progress in larval settlement and metamorphosis: closing the gaps between molecular biology and ecology. Bull Mar Sci 46:465–483

Murata M, Miyagawa-Kohshima K, Nakanashi K (1986) Characterization of compounds that induce symbiosis between sea anemone and anemone fish. Science 204:407–410

Myrberg AA, Thresher RE (1974) Interspecific aggression and its relevance to the concept of territoriality in reef fishes. Am Zool 14:81–96

Olafsson EB, Peterson CH, Ambrose WG (1994) Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. Oceanogr Mar Biol 32:65–109

Pacala SW (1989) Plant population dynamic theory. In: Roughgarden J, May RM, SA Levin (eds) Perspectives in ecological theory. Princeton University Press, Princeton, pp 54–67

Pacala SW, Silander JJA (1985) Neighborhood models of plant population dynamics I. single-species models of annuals. Am Nat 125:385–411

Pawlik JR (1992) Chemical ecology of the settlement of benthic marine invertebrates. Oceanogr Mar Biol 30:273–336

Raimondi PT (1991) Settlement behavior of *Chthamalus anisopoma* larvae largely determines the adult distribution. Oecologia 85:349–360

Robertson DR (1984) Cohabitation of competing territorial damselfishes on a Caribbean coral reef. Ecology 65:1121–1135

Robertson DR, Lassig B (1980) Spatial distribution patterns and coexistence of a group of territorial damselfishes from the Great Barrier Reef. Bull Mar Sci 30:187–203

Robertson DR, Sheldon JM (1979) Competitive interactions and the availability of sleeping sites for a diurnal coral reef fish. J Exp Mar Biol Ecol 40:285–298

Robertson DR, Hoffman SG, Sheldon JM (1981) Availability of space for the territorial Caribbean damselfish *Eupomacentrus planifrons*. Ecology 62:1162–1169

Rodriguez SR, Ojeda FP, Inestrosa NC (1993) Settlement of benthic marine invertebrates. Mar Ecol Prog Ser 97:193–207

Roughgarden J, Iwasa Y, Baxter C (1985) Demographic theory for an open marine population with space limited recruitment. Ecology 66:54–57

Roughgarden J, Gaines S, Possingham H (1988) Recruitment dynamics in complex life cycles. Science 241:1460–1466

Sale PF (1971) Apparent effect of prior experience on a habitat preference by the reef fish, *Dascyllus aruanus* (Pisces: Pomacentridae). Anim Behav 19:251–256

Sale PF (1977) Maintenance of high diversity in coral reef fish communities. Am Nat 111:337–359

Sale PF (1980) The ecology of fishes on coral reefs. Oceanogr Mar Biol 18:367–421

Sale PF, Douglas WA, Doherty PJ (1984) Choice of microhabitats by coral reef fishes at settlement. Coral Reefs 3:91–99

Schmitt RJ, Holbrook SJ (1996) Local-scale patterns of larval settlement in a planktivorous damselfish – do they predict recruitment? Mar Freshwater Res 47:449–464

Shapiro DY (1987) Inferring larval recruitment strategies from the distributional ecology of settled individuals of a coral reef fish. Bull Mar Sci 41:289–295

Shulman MJ, Ogden JC, Ebersole JP, McFarland WN, Miller SL, Wolf NG (1983) Priority effects in the recruitment of juvenile coral reef fishes. Ecology 64:1508–1513

Stoner DS (1990) Recruitment of a tropical colonial ascidian: relative importance of pre-settlement vs. post-settlement processes. Ecology 71:1682–1690

Sweatman HPA (1983) Influence of conspecifics on choice of settlement sites by larvae of two pomacentrid fishes (*Dascyllus aruanus* and *D. reticulatus*) on coral reefs. Mar Biol 75:225–229

Sweatman HPA (1985) The influence of adults of some coral reef fishes on larval recruitment. Ecol Monogr 55:469–485

Sweatman H (1988) Field evidence that settling coral reef fish larvae detect resident fishes using dissolved chemical cues. J Exp Mar Biol Ecol 124:163–174

Thresher RE (1976) Field analysis of the territoriality of the threespot damselfish, *Eupomacentrus planifrons* (*Pomacentridae*). Copeia 1976:266–276

Thresher RE (1984) Reproduction in reef fishes. Tropical fish. Hobb, Neptune, New Jersey

Tolimieri N (1995) Effects of microhabitat characteristics on the settlement and recruitment of a coral reef fish at two spatial scales. Oecologia 102:52–63

Underwood AJ, Fairweather PG (1989) Supply-side ecology and benthic marine assemblages. Trends Ecol Evol 4:16–19

Victor BC (1986) Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. Ecol Monogr 56:145–160

Waldner RE, Robertson DR (1980) Patterns of habitat partitioning by eight species of territorial Caribbean damselfishes (Pisces: Pomacentridae). Bull Mar Sci 30:171–186

Wellington GM (1982) Depth zonation of corals in the Gulf of Panama: control and facilitation by resident reef fishes. Ecol Monogr 52:223–241

Wellington GM (1992) Habitat selection and juvenile persistence control the distribution of two closely related Caribbean damselfishes. Oecologia 90:500–508

Wilkinson L (1991) SYSTAT, the system for statistics. Systat, Evanston, Illinois

Williams AH (1978) Ecology of the threespot damselfish: social organization, age structure, and population stability. J Exp Mar Biol Ecol 34:197–213

Williams AH (1980) The threespot damselfish: a noncarnivorous keystone species. Am Nat 116:138–142

Williams DM (1991) Patterns and processes in the distribution of coral reef fishes. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, pp 437–474