

Habitat selection and juvenile persistence control the distribution of two closely related Caribbean damselfishes

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Summary. On many Caribbean fringing coral reefs, two closely related and ecologically similar damselfishes, the beaugregory (*Stegastes leucostictus* Müller and Troschel) and the cocoa damselfish (*S. variabilis* Castelnau), occupy nonoverlapping vertical distributions. In St. Croix (USVI), beaugregory are very abundant in shallow water back reef habitats (1–2 m depth) while cocoa damselfish are restricted to the base of the forereef (10–15 m depth).

In this study, the roles of habitat selection at settlement and juvenile persistence were investigated to determine their influence on this pattern of zonation. Settlement events observed at intervals over a two-year period revealed that habitat selection occurred at settlement and was confined to habitats occupied by adults. In addition, differences in juvenile persistence (due to mortality and/or emigration) were found when species were translocated between depths. Over a period of 100-days, juvenile beaugregory moved from 1 m to 12 m depth suffered four-fold greater losses at the deeper sites than shallow water controls, while translocated cocoa damselfish suffered twice as many losses in shallow water than controls at 12 m depth. Despite these differences in persistence, growth rates of the two species were similar and independent of depth. These results indicate that preferential habitat selection at settlement, perhaps an evolutionary response to differential juvenile mortality, may play a deciding role in determining distributions of ecologically similar species of coral reef fishes.

Key words: *Stegastes* – Preferential settlement – Damselfishes – Habitat selection – Recruitment

both (Keough and Downes 1982; Connell 1985; Davis 1987; Raimondi 1990). For some marine species, migration (or passive transport) and differential habitat selection following initial settlement may further influence adult distributions (examples for fishes include: McFarland et al. 1985; Robertson 1988; for invertebrates: Jokiel 1990). In general, the role pre-settlement, settlement and post-settlement processes play in shaping the patterns of species distributions and abundance remains poorly understood for most marine species.

Larval preference for substrata possessing specific physical or biological characteristics have been well documented for invertebrates (Meadows and Campbell 1972; Crisp 1974; Morse and Morse 1984; Butman 1987; and many others). However, because settlement is instantaneous and most invertebrate larvae tend to settle at a very small size and are often cryptic, few field studies have conclusively linked patterns of distribution and abundance with habitat selection at settlement (exceptions include: Stoner 1990; Hurlburt 1991; Raimondi 1991). This inability to distinguish habitat selection from differential post-settlement (juvenile) mortality has hampered our understanding of the processes that account for patterns of species distributions at the population and community level (Keough and Downes 1982; Keough 1984; Underwood and Denley 1984; Connell 1985; Osman et al. 1989).

Recent studies conducted on coral reef fishes indicate that habitat selection at settlement may be a pervasive and important factor accounting for habitat segregation among similar species. Sweatman (1983; 1985) has shown that *Dasyellus* spp. juveniles settle in much higher numbers on substrata occupied by conspecifics than by heterospecifics, and are able to do so through the detection of dissolved chemical cues emanating from adults (Sweatman 1988). The advantage of this behavior appears to be dependent on the density of juveniles and the presence of conspecific adults (Forrester 1990). While survivorship and growth are generally inversely related to the density of recruits and the presence of adults, survivorship of recruits is higher when adults are present.

For marine organisms whose offspring are dispersed in the plankton, patterns of adult distribution will generally be a product of either habitat selection at settlement (preferential settlement) (e.g. Grosberg 1981, 1982; Bushek 1988; Raimondi 1988, 1991), or differential mortality following settlement (Connell 1961; Shulman et al. 1983; Olson and McPherson 1987), or a combination of

Other studies have also found that habitat selection can have potentially important consequences on post-settlement survivorship and/or juvenile growth rates (Shulman et al. 1983; Aldenhoven 1986; Jones 1987a, b, 1988).

In this paper I describe depth zonation of two common Caribbean damselfishes: the beaugregory (*Stegastes leucostictus*) and cocoa damselfish (*S. variabilis*). The contribution of settlement (i.e. within < 24 h) in establishing this pattern of zonation was evaluated by periodically monitoring daily settlement on the reef over a period of 2 years. The direct (persistence in terms of mortality and/or emigration) and indirect effects (juvenile growth) of post-settlement processes that may influence zonation were assessed by experimental manipulation. Specifically, this experiment addressed the question of whether juvenile beaugregory, moved from shallow to deeper areas, suffer slower growth or lower persistence than shallow water controls, and vice versa for the cocoa damselfish. Results of this study reveal that habitat selection at settlement is sufficient to explain zonation, while differences in persistence may indicate an underlying selective advantage promoting this spatial segregation.

Ecology of study species

Reef fishes are ideal organisms with which to investigate habitat selection since most species: i) settle at a large size (10 mm standard length or greater), ii) are active and brightly pigmented following metamorphosis, and thus quite conspicuous, and iii) become site-attached immediately following settlement. The two species in this study, the beaugregory and the cocoa damselfishes, are abundant and widespread in the Caribbean (Böhlke and Chaplin 1968). They attain a maximum size of approximately 110 mm in standard length, although cocoa damselfish tend to be slightly larger. Cocoa damselfish recruits can be distinguished from beaugregory by the presence of a larger eye spot on the dorsal fin, lemon-yellow colored ventrum (versus orange for beaugregory) and several faint dark vertical bars along the midsection of the body, which are absent on beaugregory. Although distinguishable from one another, the juveniles are so similar in appearance that they are often confused even by experienced fish investigators and, following preservation, can only be separated on the basis of minor meristic differences. The bright juvenile coloration may persist into adulthood independent of sex or reproductive condition for both species (personal observations), but usually gives way to a drab dusky appearance at adulthood (approximately ≥ 45 mm standard length).

Both species maintain an algal mat or garden which provides food and serves as a nesting site. The algal garden is defended against herbivores and egg predators. For the beaugregory, the territory generally encompasses 1 m², whereas cocoa damselfish have home ranges that can extend up to 14 m² (Gronell 1980). Diets of the two species are qualitatively and quantitatively similar (Emery 1973). Juveniles feed primarily on small benthic invertebrates (89% and 76% for beaugregory and cocoa

damselfishes, respectively), later switching predominately to algae (100 and 63%, respectively) as fish establish territories.

These species occupy similar reef habitat comprised of living and dead coral colonies but their pattern of distribution within reefs is quite different. Surveys conducted in Florida (Emery 1973), Puerto Rico and Panama (Waldner and Robertson 1980), and St. Croix (this study) indicate that the beaugregory is largely confined to shallow (< 3 m depth) back reef habitats while the cocoa damselfish is found predominantly below 10 m depth on the forereef.

Methods

The research was conducted along the fringing reef at Tague Bay, St Croix, US Virgin Islands (17°45' N, 64°42' W) between October 1987 and August 1989. Observations on settlement and experimental manipulations were made on the lagoon side of the reef flat at 1–2 m depth immediately behind the reef crest (referred hereafter as the back reef, and at the base of the forereef in 12 m depth (reef base). The shallow back reef site was composed of unconsolidated coral rubble with scattered colonies of living corals, primarily *Montastrea annularis* and *Porites porites*. Patches of sand occasionally interrupted the coral rubble/reef substrata and were colonized by the green algae, *Penicillis capitatus* and *Udotea* spp. and drifting brown algae, *Dictyota* spp. At the base of the reef, the predominant cover was *Montastrea annularis* and *Porites porites*, and was also interrupted by sand patches and scattered clumps of foliose algae. Below 12 m depth, reef structure gave way to sand sediments covered with sea grasses such as *Thalassia testudinum*, *Syringodium filiforme* and *Halodule wrightii*. A more detailed description of the biological and physical characteristics of this reef can be found in Ogden (1972) and Adey (1975).

Sampling techniques

The distribution and abundance of damselfishes were estimated along 30 m transects laid parallel to depth contours. The number of beaugregory and cocoa damselfishes were recorded within 0.5 m on each side of the transect. The type of substratum in contact with the transect line was recorded at 1 cm intervals (3000 points). Estimates of fish densities were scaled to exclude areas where topographic relief was insufficient to support algal growth and provide refuge from predators (i.e. hard substrata with holes or crevices large enough for damselfish to shelter). Scaling of density simply involved excluding substrata that lacked topographic complexity from the total area covered by the transect.

Monitoring settlement

Habitat selection at settlement was determined by following daily settlement to patch reefs over a two-week period on four separate occasions between 1987 and 1989. To minimize post-settlement migration of recruits of unknown age into and from adjacent reef areas, small circular patch reefs approximately 1.5 m in diameter and 0.5 to 0.75 m in height were constructed using various-sized pieces of live and dead coral rubble placed in sand patches 3–4 m distance from the edge of the reef. Ten patch reefs were established in the shallow back reef and another ten at the reef base. Twenty-four h prior to monitoring, all resident fish less than 20 mm standard length were removed from the patch reefs, either with anaesthetic Quinaldine, or speared. Newly-settled recruits were collected daily between 9 and 10 a.m. using anaesthetic. Prior studies indicate that damselfish settlement occurs at night (Sweatman 1985; Robert-

son et al. 1988): thus settlers were probably less than 12 h old before collection. To further verify that these fish were new recruits and not immigrants, their otoliths were examined for evidence of post-settlement growth (denoted as an abrupt change in the width of the daily otolith increment: Pitcher 1988; Wellington and Victor 1992). Since settlers were removed daily, subsequent settlement events were considered to be independent of one another.

At the same time settlement was monitored on artificial patch reefs, four vertical transects were surveyed to determine whether beaugregory and cocoa damselfishes settled outside depths occupied by adults. Transects extended along the reef slope from the reef flat (just seaward of the back reef) to the reef base covering a combined area of approximately 400 m².

Juvenile growth

Size, expressed as dry body weight and standard length, and growth rate (change in standard length with age) for naturally occurring, non-manipulated juveniles were determined for beaugregory and cocoa damselfish from back reef and reef base habitats, respectively. These data were compared with the results of the control treatment in the experimental manipulations (described below under *Translocation Experiments*). Significant differences between experimental controls and these nonexperimental data would indicate potential problems with experimental procedures, such as effects associated with translocation and handling, or availability of food on the artificial patch reefs.

The body shape for both species was evaluated by the relationship between standard length (± 1 mm) and dry gutted weight (± 0.01 mg) (specimens were dried in a convection oven at 60°C for 48–72 h). Dry weight was chosen as the unit of measure for body mass since it was subject to less variability than wet weight. Regression lines for beaugregory and cocoa damselfish were compared using logarithmic transformation of length and dry weight values to determine whether there were differences in body shape that might be related to the pattern of depth distribution. Statistical analyses was performed using analysis of covariance in the MGLH program of SYSTAT (Wilkinson 1990).

Growth rates were estimated from age (since settlement) and standard body length curves. Age was determined by counting the number of post-settlement, daily increments on the otoliths (Victor 1983; Pitcher 1988; Fowler 1989; Wellington and Victor 1992). For both species, I observed that the transition from planktonic larval existence to juvenile residence on the reef is marked by an abrupt change in the width of daily increments from wide to narrow. The daily periodicity of otolith increments has been validated for several reef fishes, including members of the genus *Stegastes* (Victor 1982; Schmitt 1984; Pitcher 1988; Fowler 1989; Thresher et al. 1989), and was verified in this study for both species by counting the number of increments accreted after marking the otolith with tetracycline (described below in *Translocation Experiments*). Details of otolith preparation and description of increment characteristics can be found in Wellington and Victor (1989, 1992). The lapillus, the medium-sized pair of otoliths, was chosen for counting increments since it provided clear lines. For fish less than 100 days old, counts were repeated (by the same observer) until three consecutive counts were within ± 2 increments (maximum of 5 counts), and within ± 4 increments for individuals from 100 to 200 days old. Data on age and size of individuals up to 45 mm S.L (size at maturity) were fitted to linear, Gompertz, power and logistic growth curves (Kaufmann 1981). The linear curve provided the best fit for both species. Differences in growth rates (age versus size) between species were statistically evaluated by analysis of covariance (Wilkinson 1990) after verification that the slopes of the regressions lines were not significantly different.

Translocation experiments

To determine if growth and/or persistence of juvenile beaugregory and cocoa damselfishes varied by depth, individuals were translo-

cated within (controls) and between (experimental) depths. Beaugregory were moved from shallow back reef to deep reef base habitats where cocoa damselfish predominate, and cocoa damselfish were moved from the reef base to shallow back reef habitats where beaugregory predominate.

To minimize migration, small patch reefs (1.5 m in diameter and 0.5 m in height), similar to those used to monitor settlement, were constructed at 1 m and 10–12 m depths 4 m distance from the reef edge in isolated sand patches. The patch reefs were established at varying intervals along a depth contour over a distance of approximately 100 meters. The shallow and deep water sites were situated immediately adjacent to one another. From preliminary trials, I found that marked juveniles (2 to 4 weeks post-settlement), once acclimated to a patch reef after 2–3 days, persisted on that reef.

For beaugregory, twenty reefs in the shallow back reef habitat served as controls (individuals were moved to patch reefs within their depth of occurrence), while another 20 reefs at 10–12 m depth were populated with individuals moved from shallow water. Because juvenile cocoa damselfish were less common and more difficult to capture, it was only possible to stock 10 control reefs in the reef base and 10 experimental reefs at the back reef site. I constructed the patch reefs in October 1987 and initiated the experiments in August of 1988. This ten-month lag period provided sufficient time for a natural assemblage of reef fauna and flora to become established, thus insuring availability of food for the juvenile damselfishes over the entire experimental period. Immediately prior to introducing translocated fish to the experimental patch reefs all other fish were removed using a fish anaesthetic and dip net. Translocated fish disappearing within two days after their introduction onto the patch reef were replaced until the population remained stable for 2–3 consecutive days. Three days before initiating the experiment, juveniles of both species were collected from reef habitats using aquarium dipnets and brought into the laboratory. During the first day of captivity, fish were held in seawater at ambient temperatures in large aerated coolers (100 l). The next day they were incubated in a 0.02% solution of tetracycline for 24 h. Tetracycline diffuses across the gill membrane and is subsequently incorporated into the otolith during calcification (Schmitt 1984). This procedure provides a permanent internal marker visible with UV fluorescence microscopy. By examining the otoliths of all fishes recovered at the end of the experiment, it was possible to distinguish control and experimental fish from both natural recruits and juveniles that may have migrated from adjacent reefs during the experiment. Unfortunately, attempts to uniquely mark individual fish by injecting dye (Alcian Blue and tattooing dye) under the skin proved unsuccessful since the dye faded within 2 weeks and mortality was 10–15%.

Following the tetracycline treatment, fish were allowed to recover in seawater for another day then transferred in individual containers to the control and experimental patch reefs. Five fish were placed on each denuded patch reef. This number represents a density of 0.35 m², which is equal to or lower than mean densities of adults and juveniles normally encountered (Table 1). For the

Table 1. Distribution and abundance of beaugregory and cocoa damselfish along the outer fringing reef at Tague Bay, St. Croix. Data are numbers of individuals (juveniles and adults) per m² ± 1 S.D. scaled to proportion of suitable habitat. Samples sizes are five 30 m² transect lines in each zone

Species	Reef zone		
	Back-reef (1–3 m)	Slope (3–10 m)	Base (10–15 m)
Beaugregory	1.75 \pm 0.35	0	0
Cocoa damselfish	0	0.01 \pm 0.01	0.38 \pm 0.17
Mann-Whitney U	25	7.5	25
test statistic Probability	0.005	NS	0.005

translocated fish, the mean standard length of beaugregory was 13.5 mm (± 3.4 SD, $n=30$, range 12–18 mm) while cocoa damselfish averaged 18.6 mm (± 2.3 SD, $n=30$, range 15–22), representing an age of approximately 30 days for both species since cocoa damselfish settle at a larger size than beaugregory. Since treatment effects were evaluated within, rather than between, species, interspecific differences in size did not confound interpretation of experimental results. Intraspecific differences between patch reefs were minimized by evenly distributing different-sized individuals among replicate patch reefs. Differences in the mean standard length among replicates ranged from 1 to 2.2 mm for both beaugregory and cocoa damselfishes.

At the end of the experiment, treatment effects on growth were measured in terms of standard length and dry body weight. To avoid pseudoreplication (Hurlbert 1984), standard length and dry weight of all individuals on a patch reef were averaged to yield a single datum for each parameter. For each species, statistical comparisons of standard length and dry weight were made between control reefs (juveniles moved within depth) and experimental reefs (juveniles moved between depths) using the Student's two-tailed t statistic (Sokal and Rohlf 1981). Persistence was defined as the proportion of individuals present on a patch reef after 100 days. For statistical purposes, proportions were transformed by angular (arcsine) transformation (Sokal and Rohlf 1981) and evaluated using Student's two-tailed t -test.

Results

Species abundance and distribution

A survey of reef habitats in Tague Bay revealed striking differences in the distribution and abundance of beaugregory and the cocoa damselfishes. A transect survey revealed that beaugregory occurred exclusively in the back reef habitat (1–2 m depth) while cocoa damselfish were encountered mainly at or below 10 m depth along the reef base (Table 1). Neither the juveniles nor adults of these two species overlapped in their distribution. Along the reef slope, between the back reef and reef base habitats, the yellowspot damselfish (*S. planifrons*) and the longfin damselfish (*S. diencaeus*) were dominant [mean densities of 0.58 ± 0.15 SD and 0.25 ± 0.12 SD individuals m^{-2} , respectively ($n=5$, 30 m^2 transect)]. Density estimates show that beaugregory (back reef) were about 4 times more abundant than cocoa damselfish (reef base) per unit of topographically suitable habitat (Table 1: Mann-Whitney U test statistic = 25; $p=0.009$).

Settlement

Daily settlement followed over several, two-week periods from 1987 to 1989 shows that settlement was significantly different between depths for both species (Table 2). With the exception of a single beaugregory that settled on a patch reef at 10 m depth in June 1988, all settlers of this species were found on shallow water patch reefs. In contrast, settlement of cocoa damselfish was only observed on patch reefs at the 10 m site. Beaugregory settled more frequently and were, overall, 4 times more abundant than cocoa damselfish (Table 2). At the same time patch reefs were monitored for settlement, daily transect surveys (covering approximately 400 m^2) were conducted

Table 2. Settlement of beaugregory and cocoa damselfishes to patch reefs at 1 and 10 meters depth. Data represent the number of fish settling to ten 1.75 m^2 patch reefs per depth over a two week period. Values in parentheses are the ranges of numbers of settlers to individual reefs. G-Test for independence performed on total number of recruits

Date	Depth	Number of settlers	
		Beaugregory	Cocoa
October 1987	1 m	12 (0–3)	0
	10 m	0	0
June 1988	1 m	22 (1–4)	0
	10 m	1	3 (0–1)
August 1988	1 m	15 (0–3)	0
	10 m	0	2 (0–1)
July 1989	1 m	18 (1–3)	0
	10 m	0	10 (0–2)
Totals	1 m	67	0
	10 m	1	15

Statistic for G-Test for Independence with Yates Correction: 62.6, $p < 0.001$

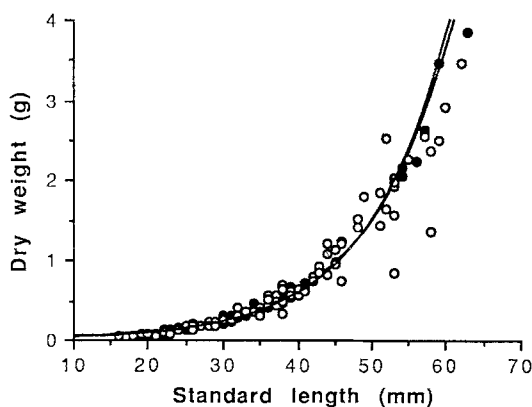


Fig. 1. Relationship between body weight and standard length for beaugregory: $y = 0.017 + x10^{0.04}$, $R^2 = 0.98$, $n = 135$; for cocoa damselfish: $y = 0.014 + x10^{0.04}$, $R^2 = 0.96$, $n = 35$. ANCOVA performed on arcsine transformed data indicated that the slopes are homogeneous, $F_{1,166} = 1.973$, $p = 0.162$, and the intercepts are not significantly different, $F_{1,167} = 2.076$, $p = 0.152$. Open circles represent beaugregory; filled circles cocoa damselfish

along the reef slope. These surveys failed to reveal any newly-settled recruits or juveniles of either beaugregory or cocoa damselfish. Settlement appeared to be differential with respect to depth for each species, and independent of the presence of adults, at least on the experimental patch reefs.

Body shape and age-length relationships

The relationship between dry weight and standard length for natural populations of beaugregory and cocoa damselfish reveal similarly shaped exponential curves for individuals over the range of 15–70 mm standard length (Fig. 1). Regression lines for dry weight and standard length (transformed to logarithms) were not significantly

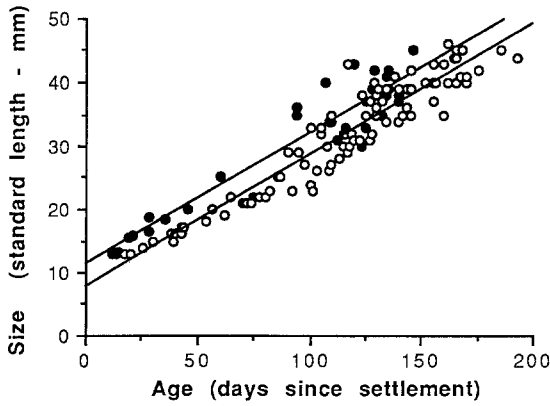


Fig. 2. Relationship between standard length and age for nonexperimental damselfishes. Age estimates based on daily, post-settlement otolith increments. Least squares regression for beaugregory, $y = 7.65 + 0.21x$, $R^2 = 0.91$, $p < 0.001$, $n = 95$; for cocoa damselfish, $y = 11.3 + 0.21x$, $R^2 = 0.92$, $p < 0.001$, $n = 40$. ANCOVA indicates that the slopes are homogeneous, $F_{1,126} = 0.033$, $p = 0.857$, but the intercepts are significantly different, $F_{1,127} = 38.19$, $p < 0.001$. Open circles represent beaugregory; filled circles cocoa damselfish

different between species indicating the body shape was similar for both species and conforms to the same pattern of growth.

Although the intercepts differed significantly due to differences in size at settlement, the curves relating age and body length (i.e. growth rates) were similar for both species (Fig. 2). Both species reach maturity at about 45 mm S.L. (beaugregory, largest immature = 48 mm, smallest mature = 40 mm, $n = 20$; cocoa damselfish, largest immature 48 mm, smallest mature = 45, $n = 15$; observations made in August 1988). Based on regression statistics, the average growth rate for juveniles of both species is approximately 0.2 mm day^{-1} (Fig. 2). Significant differences between elevations of the regression slopes for the two species reflects differences in size at settlement (Fig. 2). Data on size at settlement from the survey described above (*Monitoring settlement*) reveal that the average size at settlement for beaugregory settlers was 9.5 mm ($\pm 0.7 \text{ SD}$, $n = 76$) and cocoa damselfish 11.6 mm ($\pm 0.9 \text{ SD}$, $n = 20$), which closely approximate the intercept values for the regression lines. I interpret these results to indicate that although the two species differ in size at settlement (intercepts), their growth rates (slopes) are not significantly different. Therefore, patterns of juvenile growth appear to be the same for both species even though they live at different depths on the reef and are genetically isolated.

Growth and persistence in translocation experiments

Comparisons between translocated and control treatments for dry weight and standard length revealed no statistically significant differences (at $\alpha = 0.05$) at the end of the 100-day experiment for either species (Fig. 3). Because individuals within each replicate reef were pooled to yield a single datum, sample sizes were necessarily low, thus limiting the power of the statistical tests. Following Cohen (1969), probability of Type II errors (β)

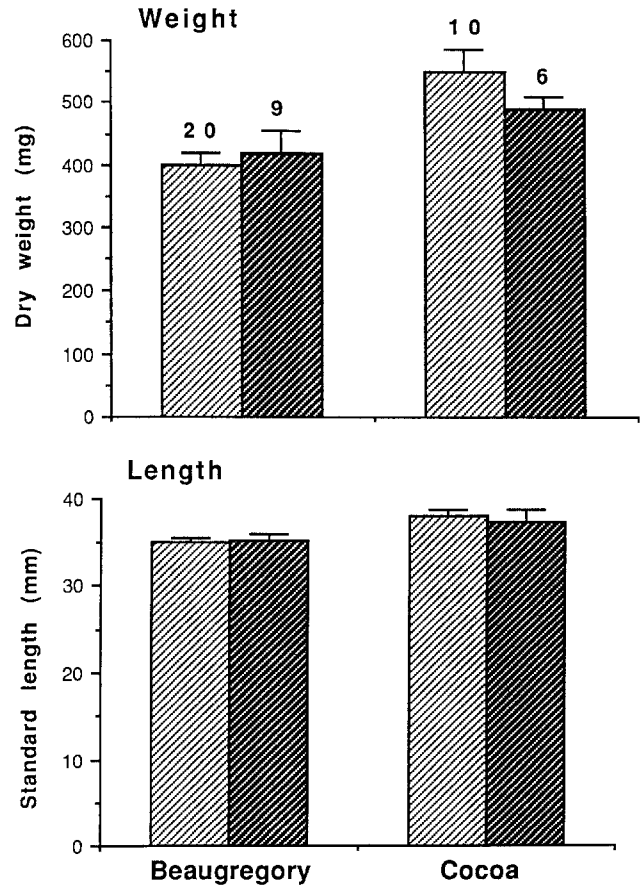


Fig. 3. Comparison of growth results for 100-day translocation experiments. Values for dry body weight and standard length are expressed as means. Error bars represent ± 1 standard error of the mean. None of the pair-comparisons were significantly different (two-tailed t tests, $\alpha = 0.05$). Each sample represents a single reef mean. Numbers above bars represent sample size

in these analyses was moderate. The power of the tests ranged from 0.40 to 0.60 (at $\alpha = 0.05$) for the six comparisons. This low power reflects the small magnitude of difference found between treatment which ranged from about 3% in standard length to 14% in dry weight. Because means were so similar, improvement in the power of these tests would have required much larger sample sizes. Since the means were not consistently higher for either treatment, there is little indication that further sampling would alter the outcome.

Using predictions generated from the regression equations for age versus length (Fig. 2), experimental fish with an age of 130 days, (initially 30 days old + 100 days on experimental reefs) would be expected to have standard lengths of approximately $34.5 \pm 1.7 \text{ mm}$ (mean \pm SD) and $38.3 \pm 1.8 \text{ mm}$ for beaugregory and cocoa damselfish, respectively. Actual overall mean values for translocated and control treatments combined were $35.2 \pm 2.1 \text{ mm}$ for beaugregory and $37.8 \pm 2.4 \text{ mm}$ for the cocoa damselfish (Fig. 3), providing additional evidence that growth in the experimental treatments was unaffected by depth.

In contrast to the similarity in patterns of growth between treatments, both species suffered significantly higher losses when translocated to patch reefs outside the

Table 3. Persistence of juvenile damselfishes on patch reefs in control and translocated treatments after 100-day experiment at Tague Bay, St. Croix. Mean values represent the proportion of original fish ($n=5$) present on each replicate reef at the end of the experiment

Species/ Treatment	<i>N</i>	Mean (± 1 SE)	Range	Degrees of Freedom	Two-tailed <i>t</i> statistic ^a	Probability
Beaugregory						
Controls (1 m)	20	0.48 (0.037)	0.2–0.8	38	6.775	$p \ll 0.001$
Translocates (12 m)	20	0.12 (0.037)	0 –0.6			
Cocoa damselfish						
Controls (12 m)	10	0.30 (0.045)	0.2–0.6	18	1.901	$p = 0.046$
Translocates (1 m)	10	0.16 (0.060)	0 –0.6			

^a *t*-test statistic based on angular transformation of proportion of fish present on patch reef

Table 4. Analysis of density effects on growth (final size) within treatments for beaugregory and cocoa damselfish in the 100-day juvenile translocation experiment. Density represents the number of experimental fish present on a patch reef at the end of the experiment. Data for control and translocated treatments are combined

Species		<i>Density (individuals per reef)</i>			
		1	2	3	4
Beaugregory	Mean dry weight (g)	0.400	0.397	0.431	0.395
	S.E. of mean	0.040	0.028	0.029	0.046
	Range: min	0.262	0.176	0.187	0.185
	max	0.592	0.655	0.645	0.609
	Sample size	8	24	21	8
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ANOVA:	Effect	d.f.	SS	F-ratio	$p > F$
	Density	3	0.015	0.288	0.834
	Error	57	1.007		
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Cocoa damselfish	Mean dry weight (g)	0.559	0.450	0.450	–
	S.E. of mean	0.039	0.068	0.060	–
	Range: min	0.303	0.196	0.270	–
	max	0.732	0.631	0.613	–
	Sample size	11	6	6	–
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ANOVA:	Effect	d.f.	SS	F-ratio	$p > F$
	Density	2	0.068	1.637	0.220 ^a
	Error	20	0.418		

^a Calculation of the power of the test to detect a difference between the three treatment means revealed a 30% chance ($\beta = 0.30$ at $\alpha = 0.05$) that the null hypothesis (that there are no differences between treatment means) will still be accepted given an actual difference in the magnitude observed

limits of their normal depth distribution (Table 3). Over the 100-day experimental period, beaugregory that were moved from 1 m to 12 m depth suffered four times higher losses at the deep site (48%) than in shallow water (12%) while the cocoa damselfish suffered approximately twice the number of losses in shallow (30%) than did controls at 12 m depth (16%).

Because of the lower persistence of fish on reefs in the translocated treatment, fewer individuals were present in this treatment at the end of the experiment than in controls. If there were density-dependent effects on growth (see Jones 1987, Forrester 1990), then the growth of individuals in the translocated treatment, with fewer individuals present, may have compensated for the potentially lower quality of the habitat. To address this potentially confounding factor, I conducted an analysis of variance to test for the effects of density (number of individuals within a patch reef) on dry weight (Table 4).

The test revealed no statistically significant differences among reefs for either beaugregory or cocoa damselfishes.

With respect to the potential effects of conspecific and heterospecific recruits to the experimental patch reefs, I could find no consistent patterns in growth or persistence among experimental reefs that were related to the number of recruits. There were few recruits (< 1 per reef) to patch reefs at the reef base, while the number of recruits to shallow patch reefs ranged from 1 to 5 at the end of the experiment.

Discussion

Although both settlement (e.g. Doherty 1983; Gaines and Roughgarden 1985; Connell 1985; Victor 1986; Underwood and Fairweather 1989) and post-settlement processes (e.g. Connell 1985; Robertson 1988; Stoner

1990) play a role in shaping patterns of distribution and abundance in marine organisms, few studies have documented habitat selection at the settlement stage (but see Grosberg 1982; Davis and Butler 1989; Sweatman 1985; Raimondi 1990, 1991). Results of this study indicate that differential settlement alone can account for the pattern of depth zonation observed in beaugregory and cocoa damselfish at St. Croix. While differential post-settlement survivorship among species within these zones cannot be entirely discounted, it is not likely to have been a significant factor since settlement was observed for fish < 24 h old. Nor is it likely that these patterns reflect preferential settlement only at low levels of recruitment [as observed in some species of barnacles (Connell 1985)], since observations were made during periods when settlement was high for one or both species. In addition, no settlement of either species was observed outside the depths of their normal adult distribution. The most detailed survey of the distribution of adult and juveniles of these species, apart from that report here, is from Waldner and Robertson (1980) in Puerto Rico. Their survey is consistent with the findings of this study: beaugregory were limited in distribution to back reef habitats at depth < 3 m, while cocoa damselfish, with the exception of a few individuals at intermediate depths (0.01 m^{-2}), were confined to depths > 9 m ($>0.1 \text{ m}^{-2}$).

Differences in fitness (i.e. early survivorship or growth) related to habitat would provide a selective force for the evolution of habitat selection at settlement. Habitat selection among invertebrates has been linked to the avoidance of potential interspecific competitors (Grosberg 1981; Young and Chia 1981), facilitation in locating conspecifics, either to reduce the threat of predators (Highsmith 1982) or ensure the likelihood of reproductive success (Jensen and Morse 1984), and for locating prey (Morse et al. 1979; Hadfield and Scheuer 1985). Among reef fishes, several studies have examined the distribution of newly-settled recruits and found evidence for habitat selection (Sale 1969; Sale et al. 1984; Sweatman 1985; Victor 1986; Jones 1987b, Carr 1991). In one case, larvae in the damselfish genus, *Dascyllus* are capable of accurately discriminating between sites through water-borne chemical cues that enable conspecifics to avoid settling next to potential competitors (Sweatman 1985, 1988). While the selective advantage of preferential settlement is unclear in most studies, Shulman et al. (1983) have shown that prior residents can have a strong influence on recruitment and subsequent juvenile survivorship in several Caribbean reef fishes.

The reciprocal translocation experiments performed here sought to evaluate whether there were species-specific differences in growth and early survivorship between depths. The lack of significant differences in either length or body weight between control and translocated treatments indicate that juvenile growth was not an important factor maintaining zonation. Possible density-dependent effects due to the variation in numbers of juveniles on patch reefs at the end of the experiment also did not appear to have been a factor influencing the results. These results, however, must be interpreted with caution since it was not known how long density varied

among replicate reefs over the 100-day experiment. Although several recent studies have shown density-dependent growth in populations of tropical reef fishes (Doherty 1982; Jones 1987a, 1989; Forrester 1990), in most of these cases juvenile densities were either higher than average, or growth was socially-mediated, rather than based on limited food supplies (see Forrester 1990). In general, it is not clear to what extent juvenile growth is affected by density-dependent factors, particularly since populations of many species appear to be regulated by recruitment rather than resources (see review in: Doherty and Williams 1988). Based on the results of my preliminary field experiments, growth of juvenile beaugregory and cocoa damselfish appeared to be independent of density and habitat. The similarity in size between experimental (manipulated) and nonexperimental (naturally-occurring) juveniles of the same age indicates that there were probably no underlying experimental artifacts that might have confounded these results.

Assuming that there were no species-specific differences in resource quality between depths that affected juvenile growth, what other factor(s) might account for preferential settlement? Lower persistence of juveniles in the translocated treatments due to mortality would certainly be a selective force. While the experimental results were consistent with a differential mortality hypothesis, emigration can not be entirely ruled out as an alternative explanation. Population studies conducted on patch reefs often equate loss of individuals with mortality since most species are considered to be sedentary in their movements, particularly territorial damselfishes that defend algal resources (e.g. Williams 1981; Doherty 1983). When migration occurs, it is largely assumed to be limited to contiguous reef habitat or between patches that are separated by short distances. Some workers have reported relocation by subadults and adults between habitat patches (Randall 1963; Robertson and Foster 1982; Choat and Bellwood 1985; Itzkowitz 1985). Forrester (1990) and Jones (1987b) have inferred substantial migration by planktivorous damselfishes between small coral patches placed as far as 11 m apart. Possible migration of surgeonfishes recruits between large patch reefs, separated by 25 m or more, has been reported by Robertson (1988). Obviously, it is possible that some of the losses reported here could have been caused by emigration, as well as predation. The contribution of these two factors need to be addressed in future studies.

In summary, the results presented here clearly show that habitat segregation among two ecologically similar species of Caribbean damselfishes is established by preferential settlement, rather than by differential persistence following settlement. No difference in juvenile growth was detected between translocated and control treatments for either species. While there were fewer losses on control reefs compared to translocated reefs, the relative importance of mortality and emigration could not be assessed. It is possible, however, that preferential settlement for both species may serve to minimize juvenile mortality.

These results contribute to the view that patterns of abundance and distribution of coral reef fishes are in-

fluenced by deterministic processes (Doherty and Williams 1988). On the Great Barrier Reef, habitat selection at settlement may explain the consistent cross-shelf patterns in adult distribution (Anderson et al. 1981; Williams and Hatcher 1983; Russ 1984) and the close match between spatial variation in recruitment and the relative abundances of adult populations (Williams et al. 1986). More studies on habitat selection at settlement will help to further define the role of preferential settlement as an important determinant of local and regional patterns of community structure in coral reef fishes.

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