SPATIAL PATTERNS OF BICOLOR DAMSELFISH POPULATIONS IN JAMAICA AND ST. CROIX ARE DETERMINED BY SIMILAR POST-SETTLEMENT PROCESSES

R. S. Nemeth

Department of Zoology,
University of New Hampshire,
Durham, NH 03824

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SPATIAL PATTERNS OF BICOLOR DAMSELFISH POPULATIONS IN JAMAICA AND ST. CROIX ARE DETERMINED BY SIMILAR POST-SETTLEMENT PROCESSES

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Department of Zoology, University of New Hampshire, Durham, NH 03824 USA

ABSTRACT

Larval supply, larval behavior and post-settlement processes all affect the abundance and distribution of marine fish populations. Post-settlement processes were found to largely determine distribution patterns of bicolor damselfish (*Stegastes partitus*). Although *S. partitus* larvae settle at similar densities to both back reef (BR) and fore reef (FR) habitats, adults are more abundant on the FR. I tested the hypothesis that similar post-settlement processes were acting among distant sites to produce this general pattern of distribution and population structure. Juvenile mortality was significantly greater on *Montastrea annularis* coral than on *Porites* rubble. This effect was similar among FR and BR habitats and between St. Croix and Jamaica. The effects of substrate type on growth was minor with some suggestion that juveniles grow faster on *Porites* rubble. Increased competition for space and decreased planktonic food reduced juvenile growth rates in BR habitats on both islands. *S. partitus* living in the BR take twice as long to reach adult size, making them more vulnerable to predation during this prolonged juvenile period. The combined effects of these factors are sufficient to reduce adult abundance on the BR thereby producing the spatial patterns of distribution observed among reef zones in this and other studies in the Caribbean.

INTRODUCTION

The dispersive larval stage of marine organisms functions to colonize patchily distributed habitats or unpredictable environments while spreading the risk of local extinction across a wide geographical range (Barlow 1981). This trait has focused attention on the importance of variation in the arrival of colonizing individuals in determining the distribution and abundance of reef fishes (Doherty and Williams 1988; Doherty and Fowler 1994). Alternative explanations have considered the effects of processes occurring after settlement in structuring populations (Smith and Tyler 1972; Talbot et al. 1978; Gladfelter et al. 1980). Recent evidence indicates that the interactions between fishes and their relationship within the physical and biological environment may prove to be important in predicting changes in population structure (Eckert 1985; Jones 1988, 1991; Forrester 1990, 1995; Hixon 1991; Robertson 1996).

When a larva makes the transition to the reef environment, its fitness will be increased if it selects a place to live where predation is minimized and growth is maximized (Gilliam and Fraser 1987). While patterns in juvenile distribution, growth and mortality have been detected in a number of reef fishes (Jones 1986,1988; Wellington 1992), the habitat characteristics responsible for these patterns and their relative importance on subsequent population structure remain unknown (Hadfield 1986; Richards and Lindeman 1987). The extent to which habitat characteristics influence population structure requires information on fish-habitat associations. For example, in a group of six ecologically similar Atlantic pomacentrids of the genus *Stegastes*, the juveniles and adults display habitat distribution patterns which are fairly consistent throughout the Caribbean (Emery 1973; Clarke 1977; Itzkowitz 1977; Waldner and Robertson 1980). The mechanisms generating these patterns at one location may include habitat selection at settlement, differential mortality after settlement, or unequal competitive abilities among species (Wellington 1992, Robertson 1996).

In this study I examine the importance of these mechanisms in affecting the distribution and population structure of *Stegastes partitus* Poey (Pomacentridae). Juveniles primarily occupy rubble substrates on back reef and fore reef habitats (Emery 1973; Clarke 1977; Itzkowitz 1977; Waldner and Robertson 1980). Adults occupy *Porites porites* and *Montastrea annularis* colonies, sponges and large rubble but are largely restricted to fore reef habitats. This unique size-class distribution was examined with recruitment surveys and with experiments measuring the variation in juvenile feeding behavior, competitive interactions, growth and survival among different habitats and substrates. The demographic responses to these conditions were measured on two islands in the Caribbean to examine the generality of the results at a larger spatial scale.

MATERIALS AND METHODS

This study was conducted in Teague Bay, St. Croix, United States Virgin Islands (17°45' N, 64°42' W) and Discovery Bay, Jamaica (18°27' N, 77°24' W). Since the population structure of *Stegastes partitus* had not been previously documented in St. Croix, juvenile and adult densities were visually sampled in back reef (BR) and fore reef (FR) habitats during July from 1991 to 1994. Juvenile and adult fish were counted along 30 x 1 m strip transects (n=16) by divers who held a 1 m wide T-shaped bar for reference. Census data on juvenile and adult abundance in BR and FR habitats were averaged for each year (n=4) and analyzed with ANOVA.

The effect of different substrate types within each habitat on juvenile growth and survival was examined in Teague Bay in August 1992 using an orthogonal experimental design. I selected four isolated *M. annularis* coral heads (1 to 1.25 m^2) and constructed four *P. porites* rubble piles (1 m^2) in sand flats in adjacent FR (10-15 m depth) and BR (1-5 m) habitats. Juvenile *S. partitus* were collected and marked with tattoo ink and treated in a 0.25 g/l bath of tetracycline hydrochloride for 12 hr to mark their otoliths (Hettler 1984). After the 16 experimental units were denuded of all fishes, the tagged juveniles were stocked at 4 fish/m^2. Fish length averaged 14.1 mm SL ($\pm$1.73 SD). During the experiment recruitment of other species was allowed to occur. The area around the study site was also censused twice for possible *S. partitus* emigrants. In only two instances, once on the BR and once on the FR, was an experimental fish found on an adjacent coral head. This occurred within the first two days after stocking so each fish was captured and returned to the nearest experimental unit, a coral head. Potential predators occupying or visiting experimental units were counted and these data were used to estimate predator densities in FR and BR study sites.

Feeding behavior (bites/min in plankton and benthos) and aggressive interactions (chases/min) were recorded for each fish during three 10 min observation periods. Aggressive encounters were grouped as intraspecific aggression (adult + juvenile *S. partitus*), interspecific aggression (all other *Stegastes* spp.) or aggression with other non-pomacentrid spp. A total of 57 hours of observations were recorded from 22 FR fish and 20 BR fish between 15 and 26 August from 08:30 to 18:30. At the end of the two week study, surviving fish were collected and their otoliths extracted. Lapillar otoliths were viewed under UV light and the distance from the tetracycline mark to the edge of the otolith was used as a measure of fish growth. Since lapillus radius (LR) was highly correlated with standard length of fish (r^2=0.90, P<0.001), it was used to calculate individual growth rate in standard length (SL) with the regression equation: $SL = -1.776 + 56.1(LR)$. The formation of daily growth increments on otoliths has been experimentally verified for *S. partitus* by (Robertson et al. 1988). Growth and behavioral data were averaged to yield a single datum point per experimental unit and analyzed using two-way analysis of covariance with zone (FR vs. BR) and substrate type (live coral vs. coral rubble) as fixed factors and standard length as a covariate. Prior to analysis data were tested for homogeneity of variances using Bartlett's chi-square (Sokal and Rohlf 1981). When necessary data were transformed ln(X + 1) to meet assumptions of homoscedasticity.

In St. Croix the relative supply of planktonic organisms available to juvenile *S. partitus* in BR and FR habitats was measured using tube traps (Yund et al. 1991). The clear, cylindrical acrylic tubes (60 cm height x 5.1 cm inside diameter) were filled with a 10% solution of buffered (borax) formaldehyde and sea water with a few drops of food color added to monitor formalin level. Twelve tube traps were deployed in pairs at each site. At the end of the study, tube traps were retrieved, filtered through a 75 µm mesh sieve and the preserved planktonic organisms from each tube were counted and classified to ordinal level.

Based on the results of this study, a similar experiment was conducted in Discovery Bay, Jamaica in February 1994. This experiment excluded tube traps but included the addition of beaugregory damselfish (*S. leucostictus*) to directly test the effects of interspecific competition on growth and survival. The experimental design included reef habitat (FR vs. BR), substrate type (*M. annularis* coral vs. *Porites* rubble) and interspecific competition (0 vs. 5 *S. leucostictus* /m^2), as main effects with four replicates per treatment. After juvenile *S. partitus* densities (4 fish /m^2) were established, juvenile *S. leucostictus* were added to half the randomly selected experimental units at 5 fish/m^2. This was the natural density of *S. leucostictus* on the BR. After four weeks, *S. partitus* were collected and growth, percent survival and feeding behavior were analyzed with a 3-way ANOVA.

RESULTS

In Teague Bay, juvenile recruitment was similar among reef habitats but adult densities were consistently greater on the fore reef (Fig. 1). Analysis of growth rates indicated that juvenile *S. partitus* living on the FR grew significantly faster than those living on the BR, but there was no detectable difference in fish growth among substrate type (Fig. 2). Variation in growth results from the difference between energy acquired (quality or quantity of food supply) and energy expended (activity rate). These differences among reef habitats were reflected in plankton trap samples, foraging patterns and degree of territorial defense.

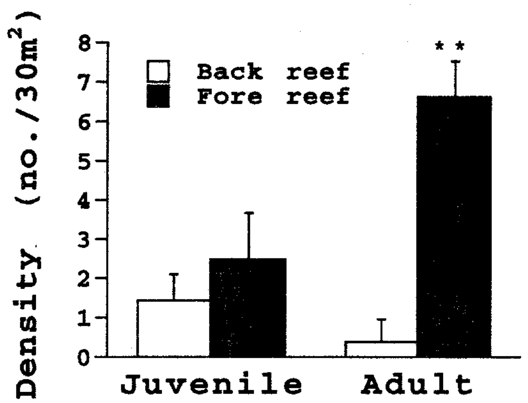

Fig. 1: Mean and standard error (s.e.) of juvenile and adult *Stegastes partitus* densities on back reef and fore reef habitats of Teague Bay, St. Croix. ** P<0.01.

Analysis of tube trap contents from St. Croix indicated that total plankton supply was 40% greater on FR relative to BR locations with copepods dominating numerically (Fig. 3). Analysis of foraging patterns indicated that juveniles living on the BR fed at higher rates on the benthos whereas FR fish spent a greater portion of their time feeding on planktonic organisms (Table 1). Among substrates, fish living on coral fed more on planktonic organisms than fish living on rubble in both BR (34% vs. 16%) and FR (59% vs. 17%) habitats. Intraspecific aggression was greater for juveniles living on the FR due to the presence of several adult conspecifics which moved onto experimental units. Conversely, interspecific aggression was higher on the BR due to recruitment of *S. leucostictus* but also *S. planifrons*. Aggression with non-pomacentrid species was similar among substrates and habitats (Table 2).

In Jamaica, patterns of growth of juvenile *S. partitus* matched those found in St. Croix. Fish living on the FR had faster growth rates than fish on the BR with no difference among substrate types (Fig. 2). Moreover, juvenile *S. partitus* showed depressed growth rates living in the presence of the territorial competitor, *S. leucostictus* (0.105±0.008 vs. 0.143±0.011 mm/d SL, $F_{1,21}$=12.59, P<0.002).

Fish survivorship was significantly higher on *Porites* rubble than on *Montastrea* coral in both Teague Bay and Discovery Bay (Fig. 4). In St. Croix, reef habitat was also important in affecting mortality rate but this effect was not apparent in Jamaica (Fig. 4). In Jamaica, the presence of *S. leucostictus* reduced survival of *S. partitus* by 18% (56% vs. 75%) but this trend was not statistically significant ($F_{1,21}$=2.32, P<0.143). All interaction terms in the 2-way and 3-way ANOVAs were non-significant at P<0.05.

Potential predators counted in St. Croix and Jamaica included large and small groupers (Serranidae), lizardfish (Synodontidae), trumpetfish (Aulostomidae), moray eels (Muraenidae), and snappers (Lutjanidae). The total density of these predators was relatively similar among reef habitats in St. Croix but very different among habitats in Jamaica (Fig. 5). In Jamaica, the graysby *Cephalopholus cruentata* was very abundant on the FR and especially effective as a predator on juvenile *S. partitus* (pers. obs.).

DISCUSSION

In Teague Bay, *S. partitus* larvae settled to both back reef (BR) and fore reef (FR) habitats at similar densities, therefore habitat selection at settlement is probably of minor importance in structuring adult populations in St. Croix. Behavioral observations of juveniles on FR and BR habitats identified potential benthic mechanisms which may have accounted for the lack of adults in BR habitats. Juveniles living on the BR had higher rates of interspecific aggression and subsequently lower rates of growth. Increased interspecific aggression on the BR of Teague Bay was largely due to settlement and immigration of the pomacentrid *S. leucostictus* onto experimental reefs. These levels of aggression (Table 4) are similar to those reported by Shulman (1985a). It is possible that as aggressive interactions escalated, growth was reduced since less time was spent feeding and more energy used for defense. The experiment in Jamaica confirmed this hypothesis with juvenile *S. partitus* growing slower in the presence of *S. leucostictus*. Moreover, *S. leucostictus* reduced persis-tence of *S. partitus* by 18% in Jamaica, suggesting that mortality can be increased from the combined effects of slowed growth and reduced vigilance for predators (Shulman 1985a,b; Booth 1995; Jakobsson et al. 1995).

The results of other studies examining the effects of interactions between pairs of species on growth and mortality have been mixed. Among non-territorial planktivorous pomacentrids *Dascyllus aruanus* had no effect on growth and survival of *Pomacentrus amboinensis* (Jones 1987,1988), whereas the presence of other planktivorous species decreased juvenile *Acanthochromis polyacanthus* survival but had no effect on growth (Thresher 1983a). Among territorial herbivorous pomacentrids *Pomacentrus wardi* and *P. flavicauda* had no effect on the other species' survival (Doherty 1982,1983) whereas *Stegastes planifrons* gained weight more slowly when in the presence of *Microspathidon chrysurus* (Robertson 1984). These varied results suggest that species-specific differences in foraging behavior, habitat use and competitive ability may determine the outcome of interspecific interactions.

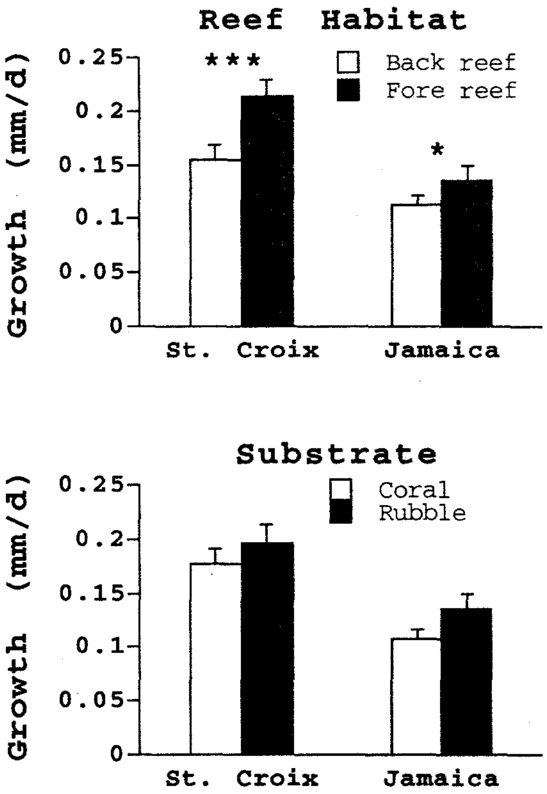

Fig. 2: Mean (+ s.e.) growth rate in standard length of juvenile *S. partitus* among reef habitats (BR vs. FR) and substrates (*Montastrea* coral vs. *Porites* rubble) in St. Croix and Jamaica. * P<0.05, *** P<0.001.

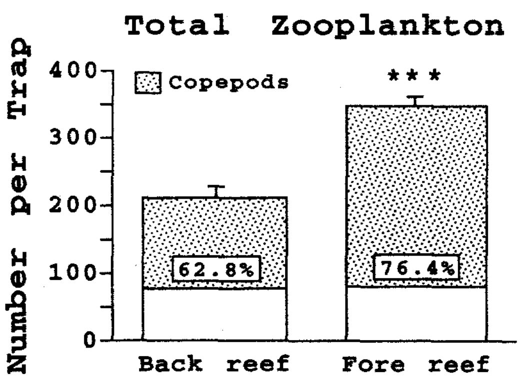

Fig. 3: Mean zooplankton density (+ s.e.) from tube traps on the fore reef and back reef of St. Croix showing percentage of copepods. *** P<0.001.

During the juvenile phase, *S. partitus* shift their diet from benthic to pelagic material indicating an increased need for planktonic food with age (Stevenson 1972; Emery 1973). Tube trap samples showed a marked reduction in planktonic organisms from FR to BR habitats which is in concordance with earlier studies (Glynn 1973; Bray 1981; Hamner et al. 1988; Kingsford and MacDiarmid 1988). Copepods, which are the only animal consistently eaten by *S. partitus* (Emery 1973), were 64% less abundant on the BR. Reductions in the supply of zooplankton due to decreases in current speed or other factors have been

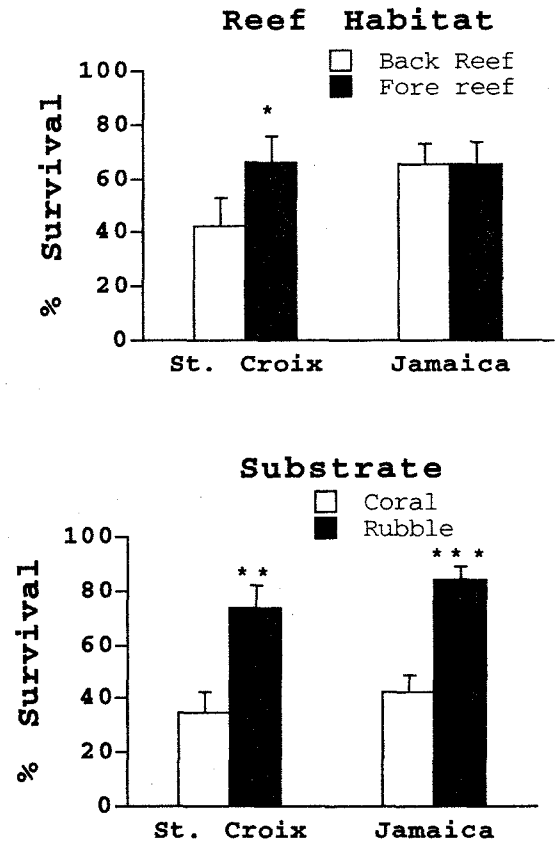

Fig. 4: Average percent survival (+ s.e.) of juvenile *S. partitus* among reef habitats (BR vs. FR) and substrates (*Montastrea* coral vs. *Porites* rubble) in St. Croix and Jamaica. * P<0.05, ** P<0.01, *** P<0.001.

Table 1: Foraging rates (+ standard error) in plankton, on benthos and % time feeding in plankton by *S. partitus* living in fore and back reef habitats on either *P. porites* rubble or *M. annularis* coral substrates. Results of 2-way ANOVA (df = 1,12) comparing habitats and substrates indicate *: P<0.05, **: P<0.01, ns: P>0.05, interaction term was ns.

	Planktonic bites/min (se)	Benthic bites/min (se)	% Time in Plankton
Habitat			
Fore Reef	4.3 (1.04)^{ns}	1.4 (0.20)*	70.3 (5.74)**
Back Reef	2.8 (0.84)	2.8 (0.55)	47.2 (7.55)
Substrate			
Coral	5.2 (1.06)**	1.6 (0.32)^{ns}	70.7 (7.76)**
Rubble	1.8 (0.17)	2.5 (0.59)	46.8 (5.31)

Table 2: Aggressive interactions (+ standard error) between juvenile *S. partitus* and conspecifics, other *Stegastes* spp., and non-pomacentrid species in fore and back reef habitats and on *Porites* rubble and *Montastrea* coral substrates. See Table 1 for statistical details.

	S. partitus chase/min (se)	*Stegastes* spp. chase/min (se)	Other spp. chase/min (se)
Habitat			
Fore Reef	0.23 (0.169)*	0.01 (0.009)**	0.04 (0.014)^{ns}
Back Reef	0.08 (0.022)	0.23 (0.128)	0.06 (0.043)
Substrate			
Coral	0.11 (0.092)^{ns}	0.19 (0.120)^{ns}	0.08 (0.048)^{ns}
Rubble	0.20 (0.079)	0.06 (0.016)	0.02 (0.009)

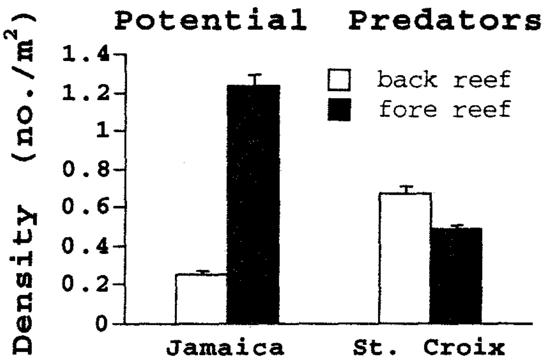

Fig. 5. Density (+ 1 s.e.) of potential predators within back and fore reef study sites in Teague Bay, St. Croix and Discovery Bay, Jamaica.

shown to influence growth and abundance of planktivorous species (Thresher 1983a,b; Jones 1986; Forrester 1990; Hobson 1991). Lower feeding rates in the plankton and reduced growth of *S. partitus* in BR habitats on both islands strongly suggests that plankton supply was limiting. Although diet overlap between *S. partitus* and *S. leucostictus* is minimal (Emery 1973), reductions in plankton supply to BR habitats may increase diet overlap between these species. However, in FR habitats where planktonic food should be more abundant, the presence of *S. leucostictus* still had a negative effect on the growth of juvenile *S. partitus* in Jamaica. Therefore, a large component of the aggressiveness between these two species consisted of defense of shelter sites.

Patterns of survival of juveniles among habitats were influenced by different processes on each island. In St. Croix, growth indirectly affected mortality due to the effects of limited food resources and elevated competitive interactions. Smaller individuals are more often displaced from their shelter sites due to size-dependent dominance hierarchies and are more vulnerable to a larger number of potential predators (Jeffries and Terceiro 1985; Shulman 1985b; Juanes 1994). Therefore, the duration of this vulnerable period is inversely proportional to the rate of growth. For example, based on growth rates from FR and BR fish, a 10 mm recruit would reach sexually maturity at 35 mm SL (Schmale 1981; Sadovy 1986) in about 3.5 months if it settled on the FR and 7 months if it settled on the BR. My limited census of potential predators suggested that predation pressure was similar among habitats in St. Croix. Thus, with predation intensity being equal, the overall risk from predators within each habitat would decrease proportionally with increasing size. In Jamaica, however, variation in intensity of predation among habitats regulated survivorship patterns. The survival advantage achieved on the FR of St. Croix, due to increased growth, was lost in Jamaica due to increased predation pressure on the FR.

Differential survivorship between rubble and coral (r>c, Fig. 4) was largely due to the architectural characteristics of each substrate (Nemeth 1996) and these effects were consistent among habitats and islands. Refuges close to the body size of a species is important for increasing prey survivorship (Hixon and Beets 1989,1993). *Porites* rubble consists of an abundance of small holes connected by a complex matrix of tunnels. In contrast, *M. annularis* colonies provide a variety of large and small crevices within their columnar-lobate morphology (Weil and Knowlton 1994). A large number of studies have shown that the structural characteristics of different substrates can influence risk of predation (Sale et al. 1980, 1984; Kaufman and Ebersole 1984; Shulman 1985b; Robertson 1988; Connell and Jones 1991; Hixon and Beets 1993). More detailed quantitative and qualitative characterization of natural substrates, and the behavioral responses of different species within those substrates, may shed light upon other factors which affect survival.

The combination of postsettlement factors in this study have the potential to severely limit *S. partitus* populations in BR habitats and can account for the patterns of population structure found among FR and BR habitats throughout this species' geographic range (Emery 1973; Clarke 1977; Itzkowitz 1977; Waldner and Robertson 1980). Whether such biological and physical factors interact to influence the distribution and population structure of other reef fishes will need to be tested (but see Jones 1991). It is likely that the relative magnitudes of such effects are more pronounced on strongly site-attached species. More mobile species will be able to migrate to those habitats that best fulfill their needs during ontogeny. The approach of detecting and examining the broader patterns within a species' geographic range will become necessary to determine the generality of benthic processes and their effects on the distribution, abundance and population structure of reef fishes.

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