

Contrasting effects of microhabitat use on large-scale adult abundance in two families of Caribbean reef fishes

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ABSTRACT: An important question for ecologists is whether the processes that influence the distribution of organisms at small spatial scales also influence the variation in abundance at larger scales. I examined the relationship between microhabitat use by individual fishes and variation in abundance among sites for the adults of 11 species of Caribbean reef fishes (6 pomacentrids and 5 scarids). At the level of individual microhabitat use, all species associated with certain substrata(um) more than would be expected at random, but not all species associated with the same substrata. The abundance of these 11 species varied greatly among 13 sites located along the northern shore of St. Croix, US Virgin Islands. Microhabitat use explained 32 to 49% of the variation in abundance among these 13 sites for 3 of the damselfish species (*Stegastes planifrons*, *S. partitus*, and *Microspathodon chrysurus*) and ~85% for a fourth damselfish, *S. dorsopunicans*. Only one parrotfish (*Scarus iserti*) showed any relationship between microhabitat use and the distribution of adult fishes among sites with approximately 50% of the variation in its abundance explained by a combination of microhabitat and distance from the eastern tip of the island. This difference between damselfishes and parrotfishes is probably related to the degree to which these families rely upon the reef substratum for shelter. These results indicate that small-scale processes can predict large-scale distributions of organisms. However, in the case of microhabitat, these results also indicate that the relationship between the species and the reef substratum must be considered.

KEY WORDS: Coral reef fish · Caribbean · Substrata · Microhabitat use

INTRODUCTION

An important question for ecologists is whether the processes that influence the distribution of organisms at small spatial scales also influence the distribution and abundance at larger spatial scales (Caley 1995). Coral reef fishes are excellent tools with which to address this question. Juvenile and adult reef fish are closely associated with the reef substratum, and most reef fish spend their demersal life within one reef, although the exact size of that patch will depend somewhat on the behavior of the species and the physical make-up of the local environment (Robertson 1988, Sale 1991a, b). Because of the close association of reef fish with the reef substratum, microhabitat use at the level of the individual fish (e.g. substratum prefer-

ences) is one factor that can influence the distribution of fishes at smaller spatial scales. However, reefs are patchy across a number of spatial scales, from the level of coral heads within reefs up to groups of reefs within regions (Sale 1991a, b). Therefore, it is important to determine whether small-scale patterns of microhabitat use influence distribution and abundance at larger spatial scales if we are to fully understand the population dynamics of these species.

Microhabitat characteristics affect the distribution of fish within reefs or locations on both coral and temperate rocky reefs (Sale et al. 1984, Ebersole 1985, Carr 1991, 1994, Levin 1991, 1993, 1994, Booth 1992, Clarke 1992, 1996, Macpherson 1994, Tolimieri 1995, 1998, Garcia-Rubies & Macpherson 1995, Caselle & Warner 1996, Green 1996, Levin & Hay 1996). Characteristics

of the reef have also been shown to correlate with diversity and abundance of fishes among reefs (Nagelkerken 1977, Luckhurst & Luckhurst 1978, Warner & Hoffman 1980, Thresher 1983, Bell & Galzin 1984, Tolimieri 1998). Many of these studies, however, have looked at only one spatial scale, and few studies have addressed the influence of habitat or microhabitat use on adult abundance at several spatial scales. Moreover, the majority of studies on coral reef fishes have examined the effects of various processes on recruitment or the demography of juvenile fishes and have ignored adult fishes (but see Forrester 1995, Robertson 1995, 1996).

In this paper, I examine microhabitat use by the adults of 11 species of Caribbean reef fishes from 2 families (Pomacentridae and Scaridae) at 2 spatial scales. My primary goal is to determine whether within-site microhabitat use predicts the distribution and abundance of adult fishes among sites. I chose to compare damselfishes and parrotfishes because they are common members of most coral reef communities and because they represent 2 different behavioral types. Damselfishes are aggressive, territorial and site attached at small spatial scales, occupying territories 1.0 to 2.0 m² in which they lay demersal eggs (Sale 1971, Thresher 1976, Kaufman 1977). Adult parrotfishes tend to be much more mobile and to move about over areas closer to 10 to 100 m² in size (author's pers. obs., Clifton 1989, 1990, 1991, Tolimieri 1998). One might expect, therefore, that microhabitat use would be less important to the larger, more mobile parrotfishes because they may be less dependent upon the substratum for shelter from predators and nesting sites. I begin by quantifying microhabitat use by individual fish in 2 different habitats on the same reef. I then determine whether the microhabitat characteristics that affect the distribution of fishes within sites are important in explaining variation in abundance among sites.

METHODS

Within-site microhabitat use. I quantified small spatial scale microhabitat use by the adults of 6 damselfishes (Pomacentridae) and 5 parrotfishes (Scaridae) on the fore-reef slope and back-reef of the Tague Bay reef, St. Croix, US Virgin Islands (17° 45' N, 64° 42' W, Fig. 1). The Tague Bay reef is a barrier bank type reef comprised primarily of dead *Acropora palmata*, live and dead *Porites porites*, and *Montastrea annularis*. The fore-reef reaches its base at approximately 10 to 15 m, where it begins to break up into patch reefs, individual coral heads, and sand. The back-reef extends to approximately 3 m.

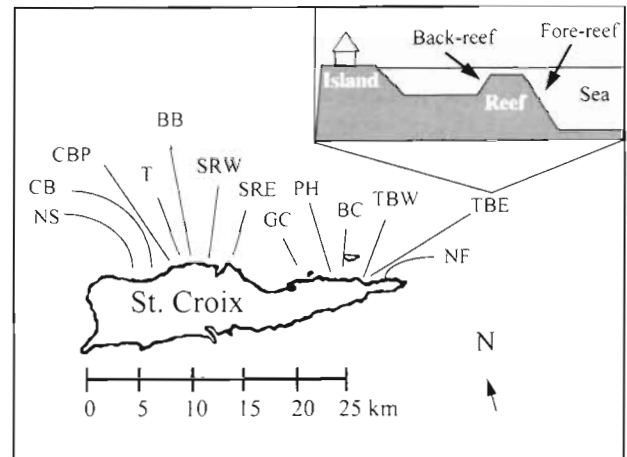


Fig. 1 Study sites, St. Croix, US Virgin Islands. NF = Nick's Folly, TBE = Tague Bay fore-reef East, TBW = Tague Bay fore-reef West, BC = Boat Cut, PH = Pink Hotel, GC = Green Cay, SRE = Salt River East, SRW = Salt River West, BB = Baron's Bluff, T = Tower, CBP = Cane Bay Point, CB = Cane Bay, NS = North Star. Small-scale microhabitat use was quantified on the fore-reef and back-reef at TBE. Inset shows a cross-section of the Tague Bay reef at TBE. Reefs west of PH are fringing reefs and do not have the same structure

Damselfish species included the three-spot (*Stegastes planifrons*), dusky (*Stegastes dorsopunicans*), longfin (*Stegastes diencaeus*), bicolor (*Stegastes partitus*), beaugregory (*Stegastes leucostictus*), and yellow-tail damselfish (*Microspathodon chrysurus*). Parrotfish species included the redband (*Sparisoma aurofrenatum*), stoplight (*Sparisoma viride*), queen (*Scarus vetula*), redfin (*Scarus rubripinne*), and striped parrotfish (*Scarus iserti*).

I used different methods to quantify microhabitat use by damselfishes and parrotfishes based on the degree to which the 2 families moved around on the reef. In both cases, however, I compare the microhabitat characteristics of areas occupied by fish to microhabitat characteristics sampled at random. Because damselfishes are highly sedentary, I used 1.0 m² quadrats to compare the substrata in areas occupied by individual fish to the substrata that were available about the reef. To sample quadrats occupied by fish, a diver set out a 30 m transect line parallel to the reef slope at 5 to 10 m depth on the fore-reef and 2 to 5 m depth on the back-reef. The diver then swam along this transect and searched for damselfishes within 1 m of either side of the transect line. When a fish was seen, the diver centered the quadrat on the location where the fish was first seen and recorded the substratum present under 49 points within the quadrat (a 7 × 7 grid). To estimate the availability of substrata, a diver sampled randomly located quadrats ('null quadrats') by swimming along a transect and placing the quadrat at predetermined,

random distances along the transect. Null quadrats sampled for substrata availability were located on transects that had already been sampled for fishes and along separate transects in the same area. Not all fish transects were sampled for null quadrats.

To quantify microhabitat use by parrotfishes, I compared the substrata that fish used (see below) during 5 min focal animal observations to the microhabitat characteristics recorded along 15 m transects. During focal animal observations, a diver followed an individual fish for 5 min and recorded the substratum the fish was over every 5 s (60 observations). Transects were laid out parallel to the reef face in the same general area. The substratum present under every 25 cm along the transect (60 points) was then recorded. During observations, the diver was careful to maintain a distance that did not disturb the subject. Any observations during which the observer felt that he had disturbed the fish were discarded. One species in particular, *Scarus rubripinne*, proved very sensitive to diver presence, and as a result, I obtained few quantitative observations for this species.

The substratum categories were the same for both the damselfishes and the parrotfishes. Percent cover of the following 9 substratum categories was recorded: *Porites*, *Porites* rubble, *Montastrea*, *Montastrea* rubble, *Acropora* rubble, live coral, boulder rubble, algae, and pavement/sand. The category '*Porites*' included living *Porites porites*, a digitate coral, whereas the category '*Porites* rubble' included dead coral that could still be easily identified as *P. porites*. '*Montastrea*' included living *Montastrea annularis*, a common massive coral, while '*Montastrea* rubble' referred to dead *M. annularis*. Likewise, *Acropora* rubble referred to dead *Acropora palmata*, a large branching coral. The group 'live coral' included all live coral except *M. annularis* and *P. porites*. The category 'boulder rubble' consisted of all unidentifiable dead coral. 'Algae' referred to all substrata heavily overgrown with foliose algae. 'Pavement/sand' referred to flat, eroded coralline rock and sand.

I used multivariate analysis of variance (MANOVA) to determine whether microhabitat characteristics differed among quadrat or transect types (species vs null). I then used contrasts (A-matrices) (Wilkinson et al. 1992) to compare each species to the randomly sampled quadrats or transects. Analyses were conducted separately for damselfishes and parrotfishes, although all species within a family were included in the same analysis. In the analyses, species were considered the independent variable, with each fish species and the null data being a category. Microhabitat characteristics were the dependent variables (the percent cover of substrata varied among quadrat or transect types, while there was only 1 fish per quadrat or observation). This is conceptually similar to doing a 1-way ANOVA compar-

ing a number of experimental treatments (fish species) to 1 control treatment (random data). To answer species-specific questions, I used individual contrasts to compare the microhabitat characteristics of areas occupied by each species to the appropriate null data (quadrats or transects). For the contrasts, p-values were Bonferroni adjusted to protect the overall experimental α . Prior to analysis, I arcsine transformed all data to control for heteroscedasticity and normality (Zar 1984, Tabachnick & Fidell 1989). I also examined the canonical loadings and plotted canonical variates from the MANOVA to investigate more closely which substrata were important in causing differences (1) between quadrats occupied by fish and null quadrats for the damselfishes, and (2) between substrata over which fish spent time and null transects for the parrotfishes.

Relationship between within-site microhabitat use and among-site abundance. To determine whether microhabitat use within sites predicted the distribution and abundance of fish at a larger spatial scale, I examined the relationship between microhabitat characteristics and fish abundance among 13 sites spanning approximately 25 km along the northern coast of St. Croix (Fig. 1). Sites were chosen primarily based on accessibility and generally included areas >2000 m² in extent. All sampling was conducted at 6 to 10 m depth, and 30 × 2 m transects were used to quantify the abundance of fishes at each site. A diver laid out a 30 m transect line and then waited several minutes before beginning to swim along the transect and recording all fish within 1 m of either side of the line. This appeared to be enough time to allow fish to return to their normal activity. The diver also recorded the substratum present under every 25 cm (120 points). These data were recorded in 3 passes along the transect. On the first pass, the diver recorded the more mobile species (parrotfishes). On the second pass, the diver counted the damselfishes, and on the third pass the diver quantified the substratum. The same substratum groupings as for the within-sites analysis were recorded, and 16 transects were done at each site.

I used forward step-wise regressions (minimum tolerance = 0.01, α to include in model = 0.15) to examine the relationships between fish abundance and microhabitat characteristics. In the analysis, I used the mean abundance of a species at each site as the dependent variable and the mean proportional cover of the substrata as the independent variables. Each species was analyzed separately. I placed 2 *a priori* limitations on the substrata included in the model: (1) prior to the analysis, I included only those substrata that influenced the species distribution within a patch, and (2) once the regression was run, I removed substrata with 'unexpected correlations' from the model and reran the analysis. An 'unexpected correlation' occurred

when a species' abundance was correlated with a substratum in the direction opposite to that which I expected based on the small-scale analyses. For example, if *Stegastes planifrons* associated with *Montastrea* within sites, I expected *S. planifrons* abundance to be positively correlated with *Montastrea* among sites. I would consider a negative correlation between *S. planifrons* and *Montastrea* cover to be an 'unexpected correlation'. If such a situation occurred, I would remove *Montastrea* from the model and re-run the analysis. I added these limitations for 2 reasons. First, my main question was whether small-scale microhabitat use affected the abundance of a species among locations. Therefore, a substratum that a species neither associated with nor avoided at a small spatial scale would not provide any information relevant to the question. Likewise, if I found an 'unexpected correlation', I could conclude that large-scale abun-

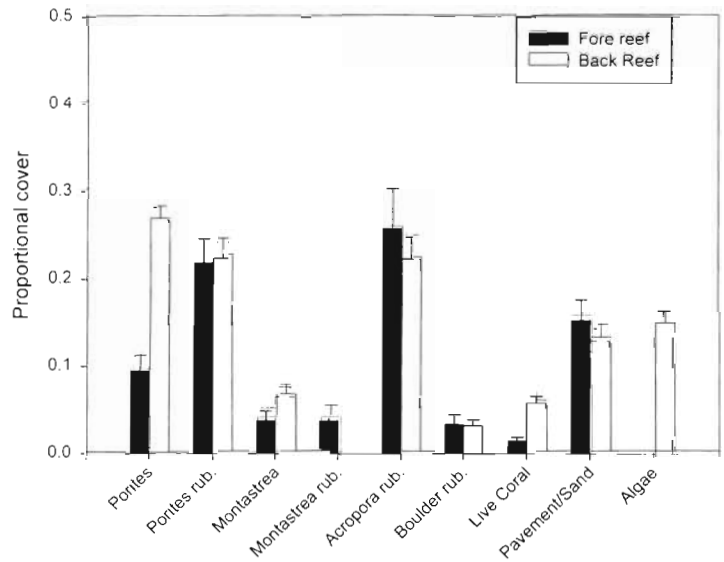
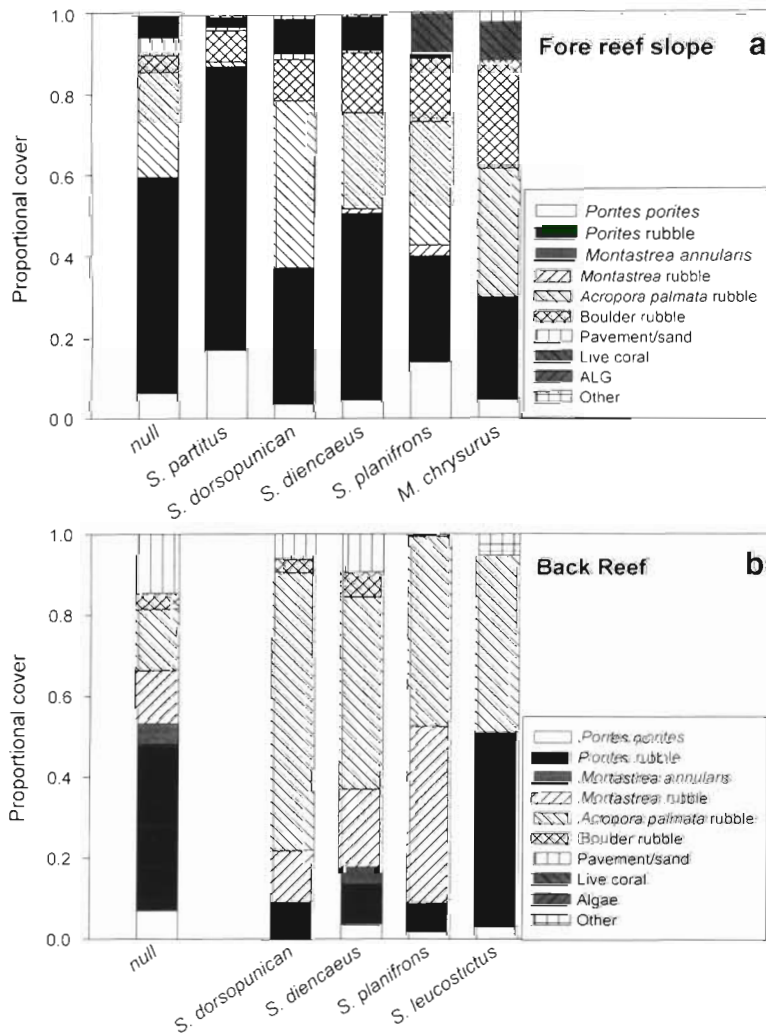


Fig. 2. Percent cover of 9 substrata on the fore-reef and back-reef at Tague Bay (rub.: rubble). See 'Methods: within-site microhabitat use' for full descriptions of substratum categories



dance was not influenced by small spatial scale microhabitat use. Second, multiple regression requires large data sets to provide robust results (Tabachnick & Fidell 1989). As the number of independent variables increases in relation to the number of replicates, the probability of chance correlations becomes more common (Tabachnick & Fidell 1989). Therefore, I wanted to eliminate any substrata whose relationships with abundance did not make sense. In the results section, however, I present the results from the first run through of the step-wise regressions and the final model with unexpected correlations removed so that the reader may evaluate both. Finally, I also included a new variable, distance from the eastern end of St. Croix (KM), to account for the spatial location of the sites. Therefore, each step-wise regression began with 4 to 5 predictor variables, but generally only 1 substratum was included in the final model.

Fig. 3. Proportional cover of 9 substrata in 1.0 m² quadrats occupied by adult damselfishes (see Table 1 for full species names) and randomly sampled null quadrats (see 'Methods: within-site microhabitat use') on the (a) fore-reef and (b) back-reef of the Tague Bay reef

Table 1. Results (p-values) of contrasts comparing microhabitat use by individual species to microhabitats available at random for parrotfish and damselfishes on the fore-reef and back-reef. n = number of quadrats or transects per species

Species	Fore-reef	n	Back-reef	n
Damselfishes				
<i>Stegastes planifrons</i>	<0.001	26	<0.001	24
<i>Stegastes partitus</i>	0.014	32		0
<i>Stegastes diencaeus</i>	0.081	21	<0.001	33
<i>Stegastes dorsopunicans</i>	0.207	29	<0.001	33
<i>Stegastes leucostictus</i>		0	<0.001	25
<i>Microspathodon chrysurus</i>	0.007	25		0
Null (random quadrats)		40		38
Parrotfish				
<i>Sparisoma viride</i>	<0.001	26	<0.001	27
<i>Sparisoma aurofrenatum</i>	<0.001	25	<0.001	19
<i>Sparisoma rubripinne</i>	<0.001	6	<0.001	6
<i>Scarus vetula</i>	<0.001	25	<0.001	19
<i>Scarus iserti</i>	<0.001	25	<0.001	24
Null (random transects)		32		32

Table 2. Canonical loadings for discriminant function analysis of small-scale microhabitat use by Caribbean damselfishes on the fore-reef and back-reef at Tague Bay (see 'Methods: within-site microhabitat use' for full descriptions of substratum categories). Data for adult damselfishes from 1.0 m² quadrats. NS = non-significant, *p < 0.05, **p < 0.01, ***p < 0.001

Substratum	Factor 1	Factor 2	Factor 3
Fore-reef			
<i>Porites</i>	0.232	-0.772	0.063
<i>Porites</i> rubble	0.888	0.035	-0.190
<i>Montastrea</i>	-0.259	-0.460	0.380
<i>Montastrea</i> rubble	-0.209	-0.348	0.605
<i>Acropora</i> rubble	-0.558	0.457	-0.212
Boulder rubble	-0.324	-0.019	0.450
Canonical correlation	0.522***	0.405***	0.275 ^{NS}
Back-reef			
<i>Porites</i>	-0.176	-0.364	-0.364
<i>Porites</i> rubble	-0.648	0.654	0.240
<i>Montastrea</i>	0.042	-0.309	-0.420
<i>Montastrea</i> rubble	0.220	0.118	-0.656
<i>Acropora</i> rubble	0.461	-0.343	0.668
Boulder rubble	-0.054	-0.021	0.037
Pavement/sand	-0.179	-0.530	-0.162
Algae	-0.205	0.067	0.057
Live coral	0.253	0.061	-0.133
Canonical correlation	0.814***	0.478***	0.360**

RESULTS

Microhabitat use within sites

Microhabitat characteristics were similar on the fore-reef and back-reef habitats at the Tague Bay reef, although live *Porites porites* was more abundant on the fore-reef at the sites sampled (Fig. 2). MANOVA indi-

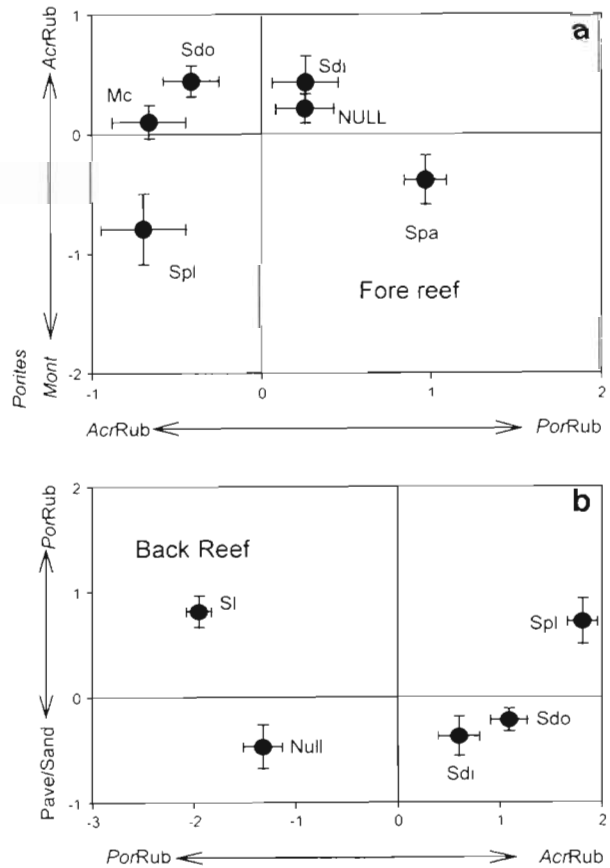


Fig. 4. Plot of the first (x-axis) and second (y-axis) canonical variates describing damselfish microhabitat use on the (a) fore-reef and (b) back-reef of the Tague Bay reef. Mc = *Microspathodon chrysurus*, Sdo = *Stegastes dorsopunicans*, Sdi = *S. diencaeus*, Spl = *S. planifrons*, Spa = *S. partitus*, SI = *S. leucostictus*. Mont = *Montastrea*, AcrRub = *Acropora* rubble, PorRub = *Porites* rubble. Error bars show ±1 SE

cated that microhabitat characteristics differed significantly among quadrat types (null vs damselfish species) on the fore-reef (Pillai trace = 0.555, df = 30, 650, $F = 3.457$, $p < 0.001$, Fig. 3a) and on the back-reef (Pillai trace = 1.105, df = 36, 554, $F = 6.064$, $p < 0.001$, Fig. 3b) (note that df = numerator df, denominator df, not a total df, i.e. 30 and 650 df not 30, 650). For the fore-reef, contrasts indicated that *Stegastes planifrons*, *S. partitus* and *Microspathodon chrysurus* associated with certain substrata more than would be expected at random (Table 1). However, *S. diencaeus* and *S. dorsopunicans* were distributed randomly with respect to substratum characteristics. Examination of canonical component loadings and plotting of canonical variates showed that adult *S. planifrons* associated with *Montastrea* and *Acropora* rubble more than would be expected at random (Fig. 4a, Table 2). *S. partitus* associated with *Montastrea* and *Porites* rubble more than would be expected at random. Finally, *Acropora* rubble was more

abundant in the quadrats occupied by *M. chrysurus* than expected.

On the back-reef, *Stegastes planifrons* associated with *Acropora* rubble and *Porites* rubble more than would be expected at random (Fig. 4b, Table 3). *S. diencaeus* and *S. dorsopunicans* both associated with *Acropora* rubble. I did not analyze the microhabitat use by *S. partitus* and *Microspathodon chrysurus* on the back-reef because these 2 species were rare. However, the beaugregory damselfish *S. leucostictus*, which is common in this back-reef habitat, occupied areas with more *Porites* rubble than expected.

Parrotfishes did not associate randomly with the substrata on the fore-reef (MANOVA, Pillai trace = 1.739, $df = 45, 645$, $F = 7.645$, $p < 0.001$, Fig. 5a) nor on the back-reef (MANOVA, Pillai trace = 1.083, $df = 45, 585$, $F = 3.594$, $p < 0.001$, Fig. 5b). Contrasts showed that, on the fore-reef, *Sparisoma viride*, *S. aurofrenatum*, *Scarus vetula*, *S. iserti* and *S. rubripinne* all associated with some substratum more than would be expected if the fish used the substratum at random (Table 1).

Examination of canonical loadings and plotting of the first 2 canonical variates showed that all parrotfish species spent more time over *Porites* rubble than would be expected at random (Fig. 6a, Table 2). In addition, *S. vetula* associated with *Acropora* rubble, and *S. iserti* utilized areas with *Porites*.

On the back-reef, relationships for parrotfishes were not as neatly separated from the null expectations, although the pattern was similar (Fig. 6b, Table 3). *Sparisoma aurofrenatum* used more pavement than was available at random. Other species tended to spend time over areas with *Acropora* rubble, while *Scarus iserti* also tended to occupy areas with pavement or sand as well.

Microhabitat characteristics and variation in abundance among sites

I eliminated 3 of the original 11 species from the large spatial scale analysis because they were not abundant enough among sites to warrant statistical analysis (Fig. 7). The species eliminated were *Scarus vetula*, *S. rubripinne* and *Stegastes leucostictus*. Microhabitat characteristics varied among sites but only *Acropora* rubble ($r = -0.567$, $p < 0.05$) and *Porites* rubble ($r = -0.571$, $p < 0.05$) were correlated with distance from the eastern tip of the island. The central sites tended to have higher percent cover of pavement or sand than other sites.

Four of the 5 damselfishes that I tested showed correlations between microhabitat use within sites and variation in abundance among sites (Table 4). Forty percent of the variation in abundance of *Stegastes partitus* among sites was explained by the percent cover of *Montastrea* (Fig. 8b). For *S. planifrons*, 96% of the variation in adult abundance among sites was explained by microhabitat characteristics, but 2 of the 4 substrata in the model showed unexpected correlations. If these 2 substrata are excluded, the percent cover of *Montastrea* (+) and the distance

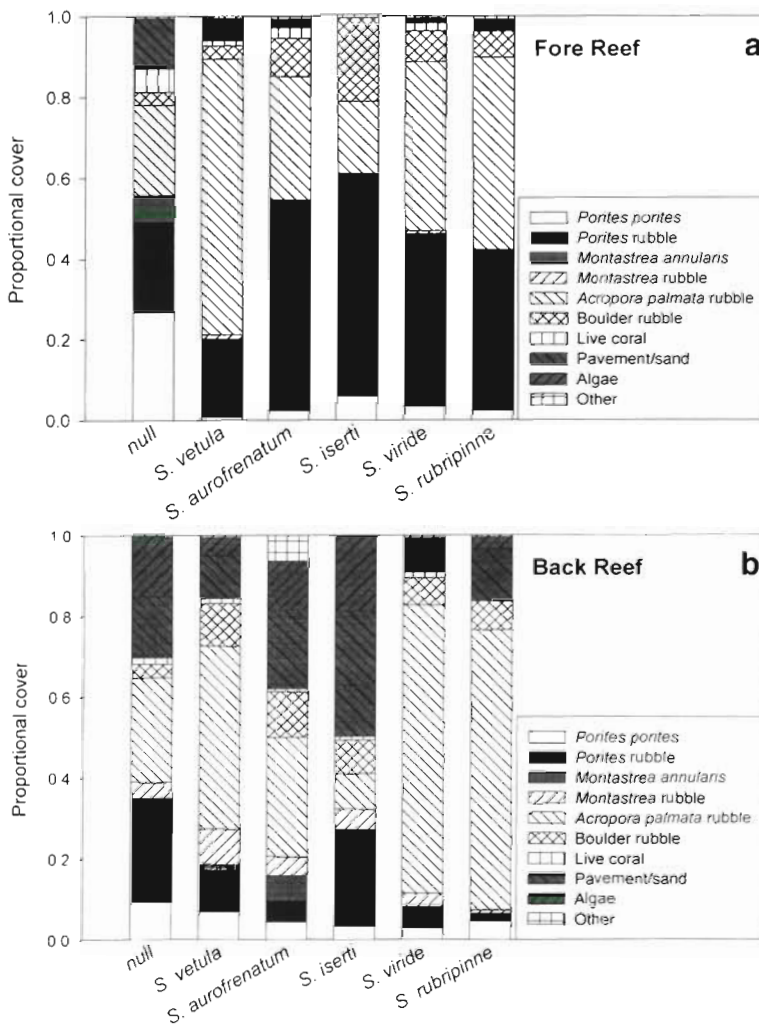


Fig. 5. Proportional cover of 9 substrata along randomly sampled null transects and the proportion of time adult damselfishes (see Table 1 for full species names) spent over those same substrata (from 5 min focal animal observations) on the (a) fore-reef and (b) back-reef of the Tague Bay reef

Table 3. Canonical loadings for discriminant function analysis of small-scale microhabitat use by Caribbean parrotfish on the fore-reef and back-reef at Tague Bay. Data for adult parrotfish are based on 5 min observations and 15 m transects.

NS = non significant, *p < 0.05, **p < 0.01, ***p < 0.001

Substrata	Factor 1	Factor 2	Factor 3
Fore-reef			
<i>Porites</i>	-0.803	-0.467	0.043
<i>Porites</i> rubble	0.281	-0.572	0.274
<i>Montastrea</i>	-0.267	0.026	-0.003
<i>Montastrea</i> rubble	0.049	0.161	-0.087
<i>Acropora</i> rubble	0.094	0.702	0.025
Boulder rubble	0.102	-0.226	-0.170
Live coral	-0.290	-0.052	0.694
Pavement/sand	-0.452	0.202	0.198
Algae	0.023	-0.003	0.118
Canonical correlation	0.875***	0.752***	0.426***
Back-reef			
<i>Porites</i>	0.164	0.488	0.033
<i>Porites</i> rubble	0.564	0.296	-0.330
<i>Montastrea</i>	0.213	0.001	0.752
<i>Montastrea</i> rubble	0.030	0.052	-0.043
<i>Acropora</i> rubble	-0.767	0.319	-0.064
Boulder rubble	-0.041	-0.316	0.061
Live coral	0.059	0.268	0.016
Pavement/sand	0.449	-0.623	0.017
Algae	0.619	-0.116	0.256
Canonical correlation	0.724***	0.517***	0.434*

from the eastern tip of St. Croix (-) explained 49% of the variation in *S. planifrons* abundance ($r^2 = 0.493$, $p = 0.034$). *Montastrea* by itself explained 35% of the distribution of *S. planifrons* among sites ($r^2 = 0.346$, $p = 0.035$, Fig. 8a). Similarly, 99% of the variation in abundance among sites of *Microspathodon chrysurus* was explained by microhabitat characteristics, but 3 of the 4 substrata included in the step-wise model were 'unexpected correlations'. If these substrata are excluded, *Acropora* rubble explained 32% of the variation in *M. chrysurus* abundance ($r^2 = 0.322$, $p = 0.043$, Fig. 8c). *S. dorsopunicans* showed the strongest correlations between habitat use and abundance. The percent cover of *Acropora* rubble and distance from the eastern tip of the island explained almost 90% of the variation in its abundance. *Acropora* alone explained 85% of the variation in *S. dorsopunicans* abundance ($r^2 = 0.842$, $p < 0.001$, Fig. 8d). *S. diencaeus* showed no correlations between microhabitat characteristics and abundance at large spatial scales (i.e. step-wise regression produced no model).

Only 1 of the 3 parrotfishes tested showed a correlation between small scale microhabitat use and large scale abundance. Within sites *Scarus iserti* associated with *Porites* rubble and avoided *Porites*, but among sites *S. iserti* abundance was negatively correlated with the percent cover of *Porites* rubble. If these 2 sub-

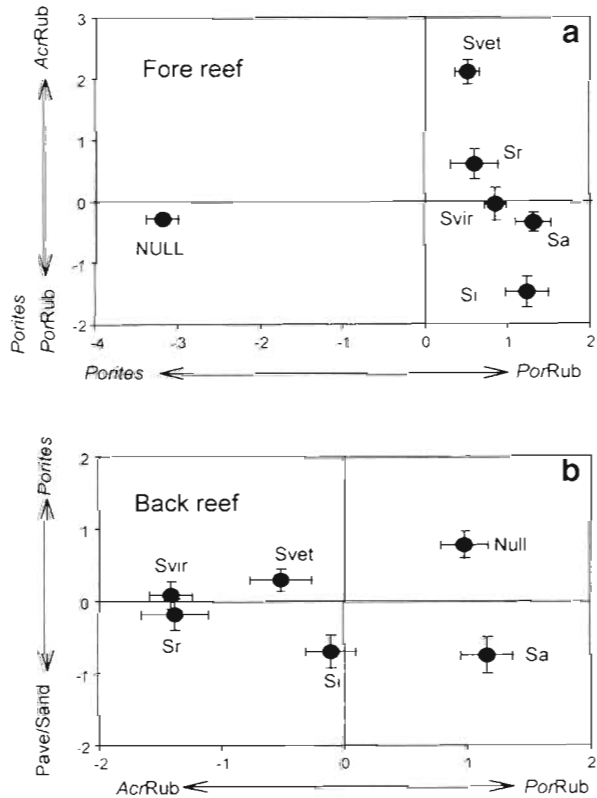


Fig. 6. Plot of the first (x-axis) and second (y-axis) canonical variates describing parrotfish microhabitat use on the (a) fore-reef and (b) back-reef on the Tague Bay reef. Svir = *Sparisoma viride*, Sa = *S. aurofrenatum*, Svet = *Scarus vetula*, Si = *S. iserti*, Sr = *S. rubripinne*. AcrRub = *Acropora* rubble, PorRub = *Porites* rubble. Error bars show ± 1 SE

strata are removed from the analysis, abundance of *S. iserti* is negatively correlated with both *Acropora* rubble and distance from the eastern tip of the island. This relationship explains 51% of the variation in abundance ($r^2 = 0.512$, $p = 0.028$). *Sparisoma aurofrenatum* showed no correlation between microhabitat characteristics and abundance among sites (Table 4). *S. viride* abundance was correlated with the percent cover of *Porites* and *Acropora* rubble, but the correlation with *Porites* was positive when it was expected to be negative. If *Porites* is removed from the analysis, there is a non-significant relationship between distance from the eastern end of the island and *S. viride* abundance ($r^2 = 0.254$, $p = 0.08$). Likewise, the abundance of *S. iserti* was correlated with *Porites*, *Porites* rubble, and distance from the eastern tip of the island, but the correlations with *Porites* and *Porites* rubble were in the opposite direction from that expected by the analysis of small spatial scale microhabitat use.

Four species showed positive correlations between abundance and total live coral cover (*Porites* + *Montastrea* + live coral) (Table 5). These species were *Spari-*

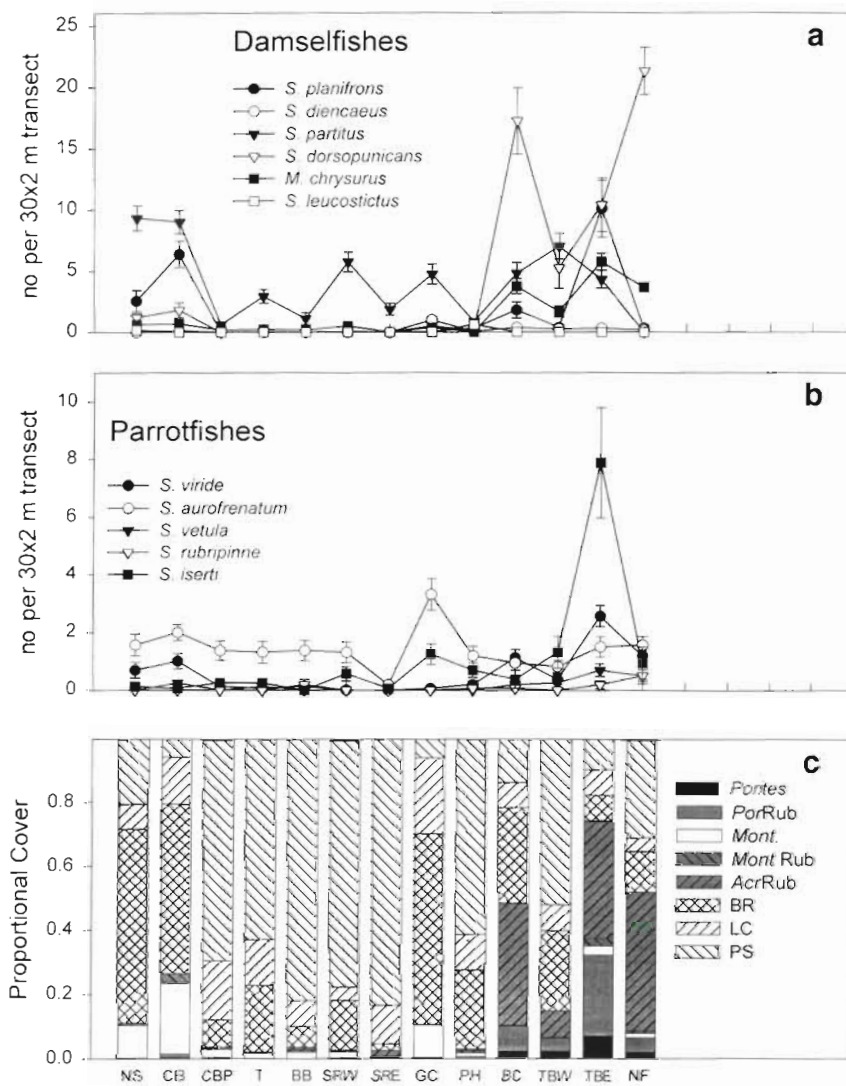


Fig. 7. Abundance of (a) damselfishes and (b) parrotfishes at 13 sites (see Fig. 1) around St. Croix, and (c) cover of 8 microhabitat characteristics at the same sites. *PorRub* = *Portes* rubble, *Mont.* = *Montastrea*, *MontRub* = *Montastrea* rubble, *BR* = boulder rubble, *PS* = pavement and sand, *LC* = live coral, *AcrRub* = *Acropora* rubble

soma viride, *Scarus vetula*, *S. iserti* and *Stegastes planifrons*. The abundances of *S. dorsopunicans* and *Microspathodon chrysurus* were correlated among sites (Table 6), but no other damselfish showed correlated distributions. The abundances of *S. viride*, *S. vetula*, and *S. iserti* were also correlated among sites (Table 6).

DISCUSSION

The majority of the species examined in this study, both damselfishes and parrotfishes, showed non-random microhabitat use at small spatial scales. When I tried to generalize these results to larger spatial scales, however, the outcome was mixed. Microhabitat use by many of the damselfishes predicted their abundances at larger spatial scales to some extent, while this was not true for the parrotfishes. The differ-

ence between damselfishes and parrotfishes is probably due to differences in the degree to which adult members of the 2 families rely upon the substrata for various resources, such as shelter from predation, nesting sites and food. The relationship between microhabitat use and large-scale abundance can also be weakened by factors such as ontogenetic changes in microhabitat use, low variation in the microhabitat among sites and processes like larval supply, that function at larger spatial scales.

Within-site microhabitat use

It is not surprising that the majority of the species in the present study showed associations with certain substrata at a small spatial scale. Non-random microhabitat use by benthic marine fishes is common in both

Table 4. Results of step-wise regression analysis to determine whether small-scale microhabitat use predicts large-scale abundance of adult fishes. The substrata included in the initial model are based on those substrata important in influencing the distribution of that species at the small spatial scale. *Scarus vetula*, *S. rubripinne* and *Stegastes leucostictus* were not tested because they were not abundant enough to allow for statistical analysis. Regressions were done only for those species that demonstrated non-random habitat use at a small spatial scale. *Por* = *Porites*, *PorRub* = *Porites* rubble, *Mont* = *Montastrea*, *MontRub* = *Montastrea* rubble, *Acr* = *Acropora* rubble, *P/S* = pavement/sand, *KM* = distance from the eastern tip of St. Croix. Bold face type indicates substrata that were correlated with fish abundance in the direction (+/-) predicted by the small spatial scale study. NS = non-significant, **p* < 0.05, ***p* < 0.01, ****p* < 0.001

Species	Factors included in analysis	Factors included in model	Coefficient	r ²
Damselfish				
<i>Stegastes planifrons</i>	<i>Por</i> , <i>PorRub</i> , <i>Mont</i> , <i>Acr</i> , <i>KM</i>	<i>Por</i> <i>PorRub</i> <i>Mont</i> <i>KM</i>	-2.08 14.44 24.84 0.08	0.96***
<i>Stegastes partitus</i>	<i>Por</i> , <i>PorRub</i> , <i>Mont</i> , <i>Acr</i> , <i>KM</i>	<i>Mont</i>	31.78	0.40*
<i>Stegastes dorsopunicans</i>	<i>Acr</i> , <i>P/S</i> , <i>KM</i> , <i>PorRub</i>	<i>Acr</i> <i>KM</i>	36.52 -0.21	0.90***
<i>Stegastes diencaeus</i>	<i>Acr</i> , <i>P/S</i> , <i>KM</i> , <i>PorRub</i>	<i>Acr</i>	7.60	0.14 ^{NS}
<i>Microspathodon chrysurus</i>	<i>Acr</i> , <i>Por</i> , <i>PorRub</i> , <i>Mont</i>	<i>Por</i> <i>PorRub</i> <i>Acr</i> <i>Mont</i>	0.11 17.07 5.82 2.12	0.99***
Parrotfish				
<i>Sparisoma viride</i>	<i>Por</i> , <i>PorRub</i> , <i>Acr</i> , <i>KM</i>	<i>Por</i> <i>Acr</i>	3.32 2.05	0.85***
<i>Sparisoma aurofrenatum</i>	<i>Por</i> , <i>PorRub</i> , <i>Acr</i> , <i>KM</i>	No model		
<i>Scarus iserti</i>	<i>Por</i> , <i>PorRub</i> , <i>Acr</i> , <i>KM</i>	<i>Por</i> <i>PorRub</i> <i>KM</i>	9.24 -11.76 -0.06	0.99***

coral reef (Sale 1971, 1972, Sale et al. 1984, Ebersole 1985, Eckert 1985, Wellington 1992, Tolimieri 1995, 1998, Caselle & Warner 1996) and temperate rocky reef systems (Holbrook et al. 1990, Carr 1991, Levin 1991, 1993, 1994, Levin & Hay 1996). Substratum is generally considered to be important in providing shelter from predation (de Boer 1978, Roberts &

Table 5. Correlations between mean adult abundance and total live coral cover among the 13 sites. Data used in the correlation analysis were mean abundance of recruits and mean percentage cover of live coral at each site. **p* < 0.05, ***p* < 0.01, ****p* < 0.001

Species	r
<i>Stegastes planifrons</i>	0.87***
<i>Stegastes partitus</i>	0.25
<i>Stegastes diencaeus</i>	0.39
<i>Stegastes dorsopunicans</i>	0.09
<i>Microspathodon chrysurus</i>	0.54 ^{0.055}
<i>Sparisoma viride</i>	0.74**
<i>Sparisoma aurofrenatum</i>	0.43
<i>Scarus vetula</i>	0.62*
<i>Scarus rubripinne</i>	0.05
<i>Scarus iserti</i>	0.85***

Ormond 1987, Hixon & Beets 1989, 1993, Hixon 1991), nesting sites (Kaufman 1977) and food resources (Kaufman 1977, Bellwood & Choat 1990).

In the present study, 8 of the 10 species demonstrated non-random microhabitat associations on the

Table 6. Correlations between species abundance among sites for damselfishes and parrotfish (see Table 5 for full species names). **p* < 0.05, ***p* < 0.01, ****p* < 0.001. Probabilities were Bonferroni adjusted within the SYSTAT statistical package

Damselfish	<i>S. planifrons</i>	<i>S. partitus</i>	<i>S. diencaeus</i>	<i>S. dorsopunicans</i>
<i>S. partitus</i>	0.416			
<i>S. diencaeus</i>	0.632	0.627		
<i>S. dorsopunicans</i>	0.228	-0.141	0.579	
<i>M. chrysurus</i>	0.622	0.016	0.626	0.840**
Parrotfish	<i>S. viride</i>	<i>S. aurofrenatum</i>	<i>S. rubripinne</i>	<i>S. vetula</i>
<i>S. aurofrenatum</i>	0.055			
<i>S. rubripinne</i>	0.468	0.028		
<i>S. vetula</i>	0.893***	0.010	0.615	
<i>S. iserti</i>	0.787**	0.105	0.262	0.755*

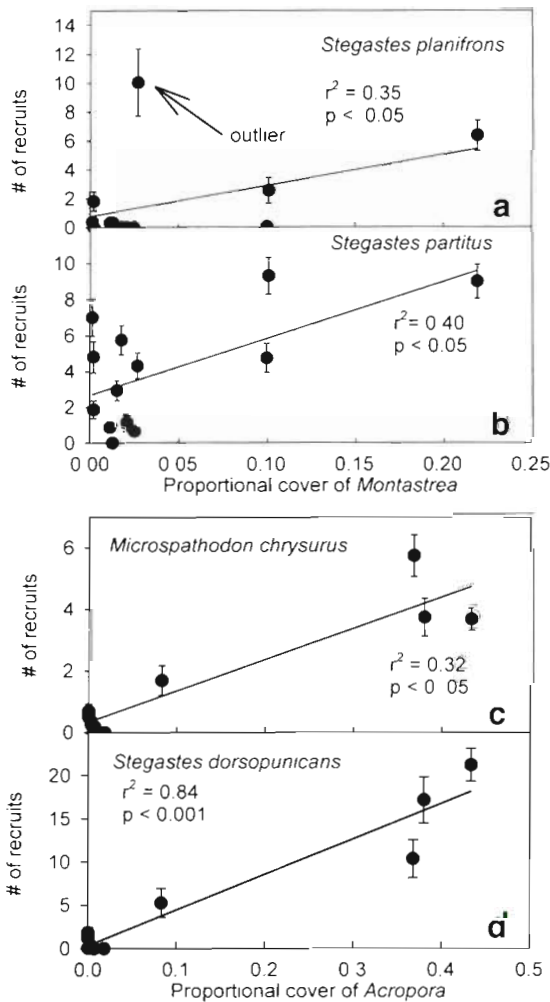


Fig. 8. Relationship between microhabitat characteristics and abundance for 4 damselfishes. These are the final models with 'unexpected correlations' removed (see 'Methods')

fore-reef, while on the back-reef all 9 species examined associated with particular substrata. Two species, *Stegastes diencaeus* and *S. dorsopunicans*, were randomly distributed on the fore-reef, while both showed non-random microhabitat use on the back-reef. *S. dorsopunicans* (~15 cm) is one of the larger damselfishes and may be more or less free from predation. However, this hypothesis is difficult to reconcile with microhabitat association by the larger *Microspathodon chrysurus* and *S. dorsopunicans*' association with *Acropora* rubble on the back-reef. The problem is probably one of power of detection since microhabitat use patterns were similar for *S. dorsopunicans* and *S. diencaeus* on the fore-reef (random) and back-reef (non-random), although the patterns on the fore-reef were non-significant.

Overall, microhabitat use was consistent between the fore-reef and the back-reef. There were some dif-

ferences, but these differences are easily explained and unimportant to the overall picture. For example, on the fore-reef, *Stegastes planifrons* associated with *Acropora* rubble in both habitats, but its association with *Porites* rubble varied between habitats. However, by using more *Porites* rubble on the back reef, *S. planifrons* was avoiding areas comprised of pavement or sand. It was positively associated with *Montastrea* in both habitats (on the back-reef *Montastrea* loaded on the third canonical variate).

Distributions and abundance among sites

Several studies have found correlations between habitat or microhabitat characteristics and adult density, but these studies have generally focused on only one spatial scale. Characteristics such as reef height (Thresher 1983), depth (Thresher 1983), reef size (Warner & Hoffman 1980), topographic complexity (Luckhurst & Luckhurst 1978, Thresher 1983, Roberts & Ormond 1987), and live coral cover (Bell & Galzin 1984, Bell et al. 1985) have been shown to be correlated with adult density. Roberts & Ormond (1987) did address spatial scale and noted that topographic complexity predicted fish abundance along 200 m transects but not along smaller 10 × 2 m transects.

Studies that have specifically addressed the interaction between microhabitat use and abundance across spatial scales present mixed results. Caselle & Warner (1996) found that the microhabitat characteristics which were correlated with the abundance of *Thalassoma bifasciatum* recruits along transects (20 × 2 m) did not explain recruitment among sites located around St. Croix. Likewise, Tolimieri (1995) saw no relationship between microhabitat choice during settlement for *Stegastes planifrons* and recruitment to 9 sites around 3 islands. In contrast, Tolimieri (1998) found that *Sparisoma viride* recruitment to 10 sites around St. Croix, St. John and Virgin Gorda (US Virgin Islands) was correlated with small spatial scale microhabitat use by recruits.

In the present study, my primary goal was to determine whether microhabitat use by individual fishes predicted the distribution and abundance of fishes among sites at larger spatial scales. Four of the 5 damselfish species that I tested showed correlations between small scale microhabitat use and large-scale abundance, which explained between 32 and 49% of the variation in the abundance of 3 species and up to 85% of the variation in a fourth. All 5 parrotfish species used the substratum non-randomly within sites, but only *S. iserti* showed a relationship between microhabitat characteristics and abundance among sites. This difference between these 2 families is probably related

to the degree to which adults rely upon the reef substrata shelter from predators, though other factors may be important as well.

Shelter from predation (de Boer 1978, Roberts & Ormond 1987, Hixon & Beets 1989, 1993, Hixon 1991) is generally considered to be important for reef fishes, but it is probably more important for damselfishes than for parrotfishes because damselfishes rely upon the substratum for a larger number of factors. Damselfishes are sedentary, inhabiting territories 1 to 2 m² in size (Sale 1971, Kaufman 1977), are deep-bodied and tend to be smaller than parrotfishes. Since territories are used as nesting sites and food resources (Kaufman 1977, Thresher 1984), damselfishes have a vested interest in staying within their territories, making them unlikely to leave when a potential threat enters their area (e.g. a diver, author's pers. obs). Damselfish territories must therefore provide sufficient shelter for individuals to avoid predators. Microhabitat characteristics may also influence the quality of nesting sites, but this should not affect local population size since local reproduction is exported (Sale 1991a, b). Parrotfishes, however, are more mobile, have a more streamlined body form, and move about the reef on larger scales of 10s to 100s of meters (Buckman & Ogden 1973, Ogden & Buckman 1973, Clifton 1989, 1990, 1991, Koltes 1993, Bruggeman et al. 1994a, b). Substratum use appears to be related to feeding preferences (Bellwood & Choai 1990) not shelter requirements (Buckman & Ogden 1973, Ogden & Buckman 1973), and since parrotfishes are pelagic spawners, the substratum is not important for nesting sites (Thresher 1984). Parrotfishes are more likely to flee, evacuate the area or maintain a minimum distance from the threat (e.g. a diver, author's pers. obs.) making shelter less important for these species. Therefore, availability of suitable substrata may limit damselfish abundance, while microhabitat use only distributes parrotfishes within sites and is unimportant for large-scale distribution.

Regardless of how strong the microhabitat requirements of a species are, we can identify a number of additional factors that may disrupt or weaken the relationship between microhabitat use and large spatial scale abundance. Ontogenetic changes in habitat and microhabitat use may weaken the relationship (Eggleston 1995, Green 1996). Large-scale patterns of adult abundance may be the result of microhabitat choice during settlement (Sale et al. 1984, Booth 1992, Tolimieri 1995) or a bottleneck effect on the survival of newly recruited fish, with adult preferences simply redistributing adult fishes within sites. This is especially likely to happen if adult substratum requirements are weak or recruitment limiting. This situation appears to be the case for *Sparisoma viride*. Recruitment of this species was higher to *Porites porites* than

to other substrata, and home range increased with increasing size (Tolimieri 1998). In the present study, its abundance was not correlated with adult microhabitat use but was correlated with the abundance of the recruit's preferred substratum (Table 4, Tolimieri 1998).

Microhabitat use may also not predict large-scale abundance if there is little variation in 'preferred substrata' at larger spatial scales. For example, Tolimieri (1995) showed that *Stegastes planifrons* selected *Montastrea annularis* during settlement, but *M. annularis* abundance was not a good predictor of *S. planifrons* recruitment among sites separated by as much as 70 km. However, there was little variation in *M. annularis* cover among sites (0 to 15% cover). In a similar study, Tolimieri (1998) showed that small-scale substratum use by *Sparisoma viride* recruits predicted recruitment at larger spatial scales. *Porites porites* (live and dead) cover, the preferred substratum, was much more variable among sites (0 to 70% cover). When variation in preferred substrata is low, microhabitat use may distribute fishes within sites, but variation in larval supply may determine abundance at larger scales. This may have been important for those species that used *Porites* rubble, which varied between approximately 0 and 25% cover among sites. However, it is less likely to have been important for those species that used *Acropora* rubble because *Acropora* rubble had higher variation in percent cover among sites (approximately 0 to 50%).

These data show that processes that function at small spatial scales, like microhabitat use, can influence distribution and abundance at larger spatial scales. Whether this occurs or not appears to depend upon a number of factors, chief of which is the degree to which particular species or families rely upon the substratum for various resources. Here, there were important differences between damselfishes and parrotfishes in how they interacted with the substratum and the effects of microhabitat characteristics on large-scale distributions. These results demonstrate that ecologists and managers working in this system need to consider not only the microhabitat characteristics of individual sites, but also how individual species of fish interact with those microhabitat characteristics across a number of spatial scales.

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