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VARIABILITY IN RECRUITMENT OF CORAL REEF FISHES: THE IMPORTANCE OF HABITAT AT TWO SPATIAL SCALES[1]

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Abstract. We investigated spatial and temporal variability in recruitment of coral reef fishes to St. Croix, U.S. Virgin Islands, with the goal of assessing the importance of habitat and physical oceanographic processes in determining patterns of distribution at two spatial scales. Recruitment was monitored visually each month, using SCUBA, at sites spaced equally around the island and on transects within each site.

Spatial patterns of distribution were consistent within seasons and between years at both spatial scales. Although recruitment showed a seasonal pattern, there were few interannual differences at any spatial scale. At the largest scale, recruitment varied significantly among sites around the island, and a unique pattern of distribution was observed. On the windward shore, recruitment ranged from high on the eastern (upcurrent) end to low on western end of the island. Recruitment showed the opposite pattern on the leeward shore, ranging from low on the eastern end to high on the western end.

At the transect scale, certain features of the habitat significantly predicted recruitment density. None of the microhabitat features that predicted recruitment at the small scale could explain patterns of recruitment observed at the large scale. In contrast, physical processes affecting larval availability or transport were more important than habitat in determining the spatial patterns of recruitment at this scale.

Thus, physical oceanographic processes appeared to be responsible for patterns of recruitment to the two shores of St. Croix, and to sites along those shores. Despite consistent patterns of recruitment to sites, habitat selection did not appear to be important at the site scale. Once delivered to a site, however, settlers or new recruits distributed themselves based on habitat preferences.

Key words: coral reef fishes; larval availability; microhabitat; recruitment variability; Saint Croix; spatial scale; Thalassoma bifasciatum; *U.S. Virgin Islands.*

INTRODUCTION

Most marine organisms and virtually all coral reef fishes have a bipartite life cycle including a planktonic larval stage and relatively sedentary juvenile and adult phases (Breder and Rosen 1966, Sale 1980). In these "open" systems, input into a local population is not expected to be directly related to the reproductive output of the same population. Thus, the distribution and abundance of reef-based individuals can be determined by events occurring independently at three distinct stages in the life of the organisms: prior to settlement, during the settlement event, or at any time after settlement. This decoupling has important consequences for the population dynamics of organisms with complex life histories and interest in these systems by ecologists has increased enormously in the last decade (Connell 1985, Roughgarden et al. 1985, Warner and Hughes 1989).

The importance of pre-settlement vs. post-settlement processes in determining adult population size has been widely disputed. Early models for coral reef fish populations stressed reef-based density-dependent processes such as competition for limiting resources (e.g., Smith and Tyler 1975, Gladfelter and Gladfelter 1978, Anderson et al. 1981). These ideas were later eclipsed by the paradigm of recruitment limitation (Williams 1980), which assumes that recruitment is generally too low to lead to saturation of reef resources and populations are thus controlled by pre-settlement processes determining recruitment levels. However, a consensus view is emerging that the ultimate abundance and distribution of reef fishes may be influenced by both pre- and post-settlement events. Hence, a better understanding of the conditions when each is likely to act is needed (Warner and Hughes 1989, Jones 1990).

Although recent studies of marine invertebrates and fishes stress the importance of recruitment, we still know very little about the processes that lead to successful settlement onto reefs. Is it a simple matter of physical processes placing larvae into a generally acceptable place at the right time, or are specific habitat requirements more important? The generally accepted view is that variation in settlement is determined primarily by availability of larvae (Victor 1984, 1986, Gaines et al. 1985, Doherty and Williams 1988, Milicich et al. 1992, Meekan et al. 1993, Gaines and Bertness, *in press*). Availability of larvae to a site can be affected by a variety of physical transport processes

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such as drift with prevailing currents (Hauri et al. 1978, Victor 1984, Williams et al. 1984, Cowen and Castro 1994), wind-induced current reversals (Gladfelter et al. 1978), aggregation due to internal waves or tidally induced fronts (Shanks 1983, Kingsford and Choat 1986, Shanks and Wright 1987, Kingsford et al. 1991), and retention features such as eddies (Hamner and Hauri 1977, Alldredge and Hamner 1980, Leis 1986, Lobel and Robinson 1986, Shapiro et al. 1988, Lobel 1989, Boehlert et al. 1992, Shultz and Cowen 1994).

Successful recruitment into a population depends not only on events occurring during the planktonic phase but also during and just after the settlement event. The exact definition of recruitment varies from taxon to taxon and from study to study. For many invertebrates, recruitment into the reef-based population may occur from hours to days after settlement. For coral reef fishes, "recruitment" is usually considered to be the time at which a fish is first observed on the reef. Thus "recruitment" may be anywhere from days to months after "settlement." We know that larvae do not behave as passively as once assumed. Some fish larvae are very active swimmers (Stobutzki and Bellwood 1994) and newly settled individuals have been shown to preferentially settle in particular habitats (Williams and Sale 1981, Sweatman 1983, 1985, Eckert 1985, Jones 1987, Booth 1992). In addition, newly settled fish may move to preferred habitat prior to their being observed on the reef. Thus spatial recruitment patterns may simply reflect the distribution of preferred habitat. The scale over which habitat selection occurs will probably vary among taxa but is little understood at this point. Suitable habitat for settlement may vary within a small area (e.g., a portion of a reef), or on much larger spatial scales. While larvae may have the ability to assess settlement cues at small scales, they may not be able to "choose" at larger spatial scales.

Densities of reef fish and invertebrate recruits have been shown to vary on a number of spatial scales: patch reefs or sites separated by tens or hundreds of metres (Luckhurst and Luckhurst 1977, Doherty 1983, Williams 1983, Caffey 1985, Raimondi 1990, Fowler et al. 1992), reefs or sites separated by several kilometres (Williams and Sale 1981, Doherty 1983, Sale and Douglas 1984, Victor 1984, Raimondi 1990), and regions separated by hundreds or thousands of kilometres (Eckert 1984, Sale et al. 1984, Victor 1984, Caffey 1985, Cowen 1985, Doherty 1987, Doherty and Williams 1988, Fowler et al. 1992). Recruitment also varies on a number of temporal scales: interannual (Hawkins and Hartnoll 1982, Williams 1983, Eckert 1984, Sale et al. 1984, Caffey 1985, Walsh 1987), seasonal (Caffey 1985, Walsh 1987, Robertson 1990), lunar (Doherty 1983, Robertson et al. 1988, Robertson 1992), and diel (Doherty 1983). Some of these scales may reflect substrate differences, while others may be correlated with physical processes. As virtually all ecologists would agree, the choice of scale of a study is crucial to the interpretation of the results (Dayton and Tegner 1984, Levin 1988). With careful interpretation of the correlates of spatial and temporal variation at a range of scales, we can better understand the causes of that variability and ultimately increase our understanding of the role of recruitment in population dynamics (Doherty 1987, Fowler et al. 1992).

The specific goals of this study were twofold: 1) to describe the patterns and correlates of recruitment of coral reef fishes to St. Croix, U.S. Virgin Islands at several spatial and temporal scales and 2) to evaluate the importance of variation in habitat to recruitment of one species, *Thalassoma bifasciatum,* at two spatial scales. Specifically, we tested two hypotheses: a) that habitat features will be more likely to influence recruitment patterns at a smaller spatial scale (transects within sites) than at a larger scale (sites around the island) and b) that physical processes affecting larval availability will more likely affect larger scale than smaller scale patterns. We also emphasize the importance of conducting studies of recruitment variability simultaneously at multiple scales by presenting interpretations of our dataset when analyzed at only the larger scale.

METHODS

Study area and species

This study took place in St. Croix, U.S. Virgin Islands (17°45′ N, 64°35′ W) from June–October of 1991 and May–November of 1992. St. Croix is a sedimentary island located in the northeastern Caribbean, inside the arc formed by the Lesser Antilles (for a complete description of the geology and reefs of St. Croix, see Hubbard 1989).

Spatial and temporal patterns of abundance are described for two groups of fishes: (i) bluehead wrasse, *Thalassoma bifasciatum,* the numerically dominant species and (ii) all other fish species (hereafter referred to as "other species"). The role of habitat in determining patterns of recruitment at two spatial scales was investigated for *T. bifasciatum* only.

T. bifasciatum is a short-lived, sex-changing labrid, common on shallow reefs throughout the Caribbean. It spawns daily throughout the year at St. Croix (Warner and Schultz 1992). Individuals settle after spending an average of 47.16 ± 0.36 d in the plankton (mean ± 1 SE), at which time new recruits are ≈9 mm standard length (SL). New recruits remain near the benthos, preferring low-relief rubble or pavement habitats until they reach sexual maturity at ≈35 mm SL. At this time they move up into the water column, switch to a more planktivorous diet, and school with other adults (J. E. Caselle, *personal observation*).

Victor (1986) found that settlement of *T. bifasciatum* in Panama tended to occur near the new moon. To verify lunar periodicity in our study, we made collections of recruits from around the island once every two

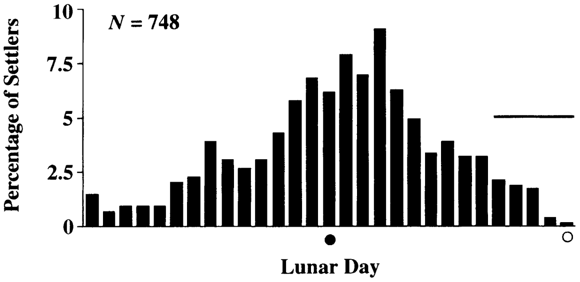

FIG. 1. Frequency distribution of settlement of *Thalassoma bifasciatum* on St. Croix, U.S. Virgin Islands, classified by lunar day. For this sample, 74.2% of all settlement occurred in the 2 wk surrounding the new moon. ○ = full moon, ● = new moon. Horizontal bar represents range of census-start days in the present study (mean starting date = 13 d past new moon).

weeks from April to October in 1992. Settlement dates were calculated from daily otolith increment counts following the procedure described in Victor (1982). Settlement in St. Croix also occurred in pulses centered near the new moon of each month (Fig. 1).

Description of spatial scales

Recruitment was observed at two spatial scales: island-wide (sites around the island) and within-site (transects within sites).

Large (island-wide) scale.—We established eight study sites, each encompassing ≈500 m². Sites were equally spaced (≈7 km from one another) around the island. All sites were located on or near the outer reef slope and were primarily composed of flat coral pavement with sparse patches of living corals (*Acropora palmata, Millepora* spp., *Porites* spp., *Montastrea* spp., *Diploria* spp.), dead corals (*Montastrea annularis, A. palmata*), and interspersed sandy areas. There were four sites on the north or leeward shore, one site on the west end, and three sites on the south or windward shore (Fig. 2). The west end, Butler Bay, is considered part of the north shore for all analyses. No sites were established on the western part of the south shore because of the lack of coral reef habitat in that area. In 1991, the westernmost site on the south shore, Ha'penny, was censused irregularly due to inclement weather conditions during that year. Consequently, we did not include this site in the analyses of temporal coherence.

Small (within-site) scale.—At each site either five or six permanent linear transects (20 × 2 m) were established. All transects were placed haphazardly within each site at the beginning of the study. Transects were placed in a roughly linear array, one after another, and all were at least 25 m away from any other. Physical characteristics of the transects generally reflected the habitat of the site. However, since each transect was essentially a subset of the site and was placed randomly within the site, a given transect may have been primarily composed of one substrate type or another (i.e., pavement, sand, live coral, dead coral, or rubble). All transects were 3–5 m in depth.

Physical habitat measurements

We measured microhabitat characteristics of every transect using a standard point-contact technique. At every 1-m interval along the transect line, three points were located, one point on the line and two points each 0.5 m away from the line on opposite sides. Thus, a total of 63 points were measured on each transect. At each point, we recorded the substrate type and complexity. Substrate measures consisted of pavement, sand, living coral, dead coral, small coral rubble (pieces ≤15 cm in length or width; e.g., *Porites* rubble) and large rubble (pieces ≥15 cm in length or width; e.g., fallen *Acropora palmata*). Complexity was measured

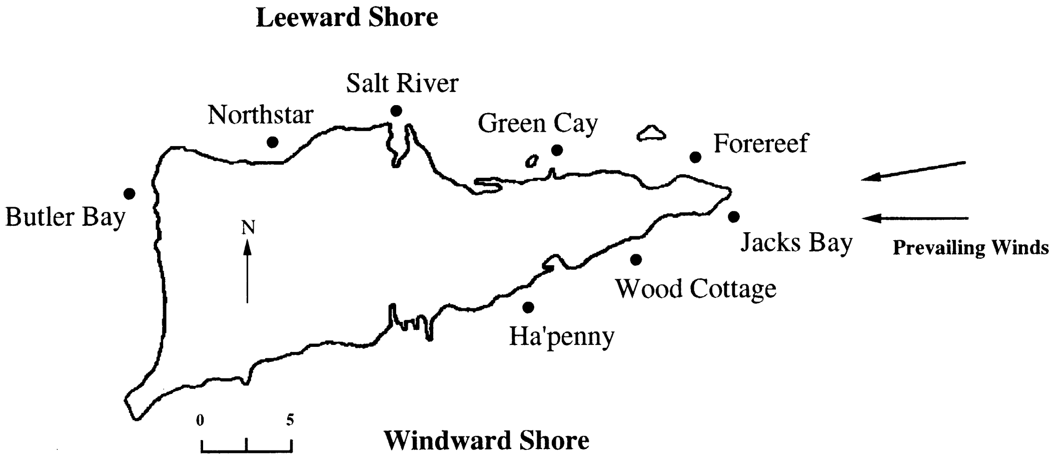

FIG. 2. Map of St. Croix, U.S. Virgin Islands, showing the locations of the eight study sites. Transects are located within sites. Prevailing winds and currents are out of the east or southeast.

as the number of times an imaginary vertical line through the point passed from water to coral and back to water (see Wiens and Rotenberry 1981, Choat and Bellwood 1985). For example, flat pavement was scored as 1, whereas a branching coral would be scored as >1 depending on the degree of branching. We also estimated rugosity (by running a small-linked chain down the center of each transect, conforming the chain to the substrate and measuring the total length of chain laid out), and water depth. These data were recorded on all transects at all eight sites. Site totals are expressed as percentage cover of each substrate variable (summed over all transects), average water depth, average rugosity, and total complexity. Percentage cover data were arcsine transformed for statistical analyses where necessary.

Recruitment surveys

Newly settled fishes were visually censused monthly by two observers on each transect at each site. To minimize the effects of temporal variation in recruitment around the island, censuses for a given month were completed at all sites in a ≤5-d period commencing 10–14 d following the new moon of each month (mean start day was 13 d past new moon). Since most settlement occurred near the new moon of each month (Fig. 1), sampling shortly after each new-moon pulse minimized the potential for underestimating recruitment due to post-settlement mortality. New recruits (i.e., fish who had settled in the month since the previous census) were distinguished from older fish based on their size, behavior, and location. These size estimates were taken from the literature and verified by otolith analysis when possible.

Analyses and Results

Spatial and temporal patterns of recruitment

Recruitment abundance is expressed throughout this paper as density of recruits (fish/m^2). Spatial and temporal variation in recruitment were analyzed separately using two-factor nested ANOVA. Recruit densities were compared spatially among sites and transects with transects nested within sites, and temporally among years and months with months nested within years. Site, year, and month were considered fixed effects and transect was considered a random effect. Because of uncontrolled differences in habitat or other environmental variables between the windward and leeward shores, most analyses were done on the two shores separately.

During the two years of monitoring, a total of 13 095 recruits of 15 fish families were censused on the transects. The dominant families were Labridae (81.7% of recruits), Gobiidae (8.3%), and Pomacentridae (5.2%). A total of 34 species were counted during the two years, 27 in 1991 and 29 in 1992. *Thalassoma bifasciatum* constituted 74.1% of all fish recruits censused in the two years combined. The next six most abundant species were a labrid, *Halichoeres bivittatus* (733 individuals), the gobies *Gnatholepsis thompsoni* (666 individuals) and *Coryphopterus glaucofraenum* (350 individuals), a pomacentrid, *Stegastes partitus* (327 individuals), a group of unidentified sparids (294 individuals), and the pomacentrid *Stegastes diencaeus* (214 individuals).

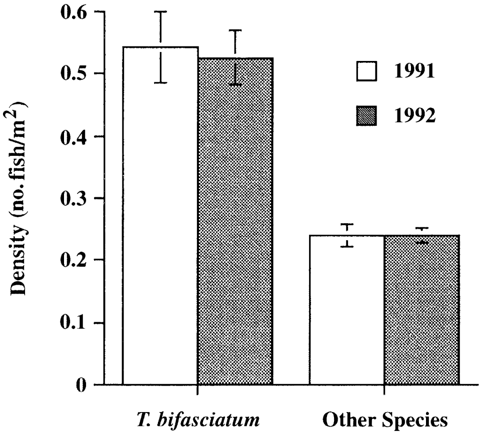

FIG. 3. Monthly recruit density of *Thalassoma bifasciatum* and other fish species in 1991 and 1992 (means ± 1 SE pooled over all eight sites).

Variation in time: among years

Whole island.—Recruit abundance in 1991 was nearly identical to that seen in 1992 (Fig. 3). There were no differences in the average density (averaged over all censuses per year for all sites) between 1991 and 1992 of either *T. bifasciatum* or other species (Student's *t* test; *T. bifasciatum*: $t = 0.23$, $P = 0.82$, other species: $t = 0.04$, $P = 0.97$).

Within shores.—Total recruit abundance on the north shore was consistent between years for *T. bifasciatum* and for other species (Tables 1a and 2a, Fig. 4). On the south shore, there was significantly greater recruitment of *T. bifasciatum* in 1991 than in 1992 (Table 1a, Fig. 4) but no interannual difference for other species (Table 2a, Fig. 4). The greater average density of *T. bifasciatum* was primarily due to one extremely large pulse of recruitment on the south shore in August of 1991 where densities >2.5 fish/m^2 were reached.

Within sites.—Between-year variation in abundance within individual sites was also low. Only three sites out of eight (Butler Bay, Jacks Bay, and Green Cay) showed significant interannual differences in *T. bifasciatum* recruitment (averaged over all censuses in each year; Fig. 5) and two of eight (Butler Bay and Northstar) showed interannual differences in other species (Fig. 5). With the exception of Butler Bay, at each of the three sites where there was a significant difference in recruitment between years, recruitment was greater in 1991 than 1992. Butler Bay, on the other hand, had

TABLE 1. Summary of analysis of variance results for comparisons of temporal (a) and spatial (b) variation of recruitment densities of *Thalassoma bifasciatum* on St. Croix, U.S. Virgin Islands. Analyses were done separately on the two shores. Variance components were calculated as per Winer et al. (1991).

a) Temporal

	Source	df	MS	F
North shore	Year	1	0.575	1.09^{NS}
	Month(Year)	10	1.910	3.62**
	Error	312	0.527	
South Shore	Year	1	8.069	32.24**
	Month(Year)	9	3.439	13.74**
	Error	118	0.250	

b) Spatial

	Source	df	MS	F	% variance
North shore	Site	4	11.897	42.96**	17.7
	Transect(Site)	25	1.958	7.07**	15.7
	Error	294	0.277		27.6
South shore	Site	4	6.756	18.46**	14.7
	Transect(Site)	12	0.665	1.82*	3.4
	Error	114	0.366		36.6

* $P < 0.05$; ** $P < 0.01$; NS = $P > 0.05$; df = degrees of freedom; MS = mean square.

TABLE 2. Summary of analysis of variance results for comparisons of temporal (a) and spatial (b) variation of recruitment densities of other species.† Analyses were done separately on the two shores. Variance components were calculated as per Winer et al. (1991).

a) Temporal

	Source	df	MS	F
North Shore	Year	1	0.034	0.82^{NS}
	Month(Year)	10	0.313	7.61**
	Error	311	0.041	
South Shore	Year	1	0.019	0.95^{NS}
	Month(Year)	9	0.248	12.70**
	Error	118	0.019	

b) Spatial

	Source	df	MS	F	% variance
North Shore	Site	4	0.311	7.51**	0.3
	Transect(Site)	25	0.106	2.56**	0.6
	Error	293	0.041		4.1
South Shore	Site	2	0.534	18.64**	1.0
	Transect(Site)	12	0.018	0.64^{NS}	0.0
	Error	114	0.041		2.8

* $P < 0.05$; ** $P < 0.01$; NS = $P > 0.05$; df = degrees of freedom; MS = mean square.

† Of 15 families, mostly Labridae (81.7% of recruits), Gobiidae (8.3%), and Pomacentridae (5.2%).

greater recruitment of both *T. bifasciatum* and other species in 1992.

Variation in time: within years

Within sites.—The amount of recruitment to sites varied from month to month for both *T. bifasciatum* (Fig. 6) and for other species (Fig. 7). Although absolute densities were different among sites, the seasonal patterns were conserved among sites on a given shore. This pattern is most apparent for *T. bifasciatum* (Fig. 6).

Within shores.—There was substantial seasonal (month to month) variation on both shores within both years for *T. bifasciatum* (Table 1a) and for other species (Table 2a), although the seasonal patterns appeared different in the two years (Fig. 8a–d). In 1991, for both *T. bifasciatum* and other species, the timing of recruitment was similar between the two shores of the island, with recruitment reaching greatest densities in either August or September and tapering off by October (Fig. 8a, c). In August of 1991, there was one large pulse of recruitment to the south-shore sites resulting in the extremely high average density of 2.68 *T. bifasciatum*/m^2. Although recruitment of *T. bifasciatum* was also greatest in August on the north shore, there was no pulse of the magnitude observed on the south shore. The south-shore August pulse, although primarily composed of *T. bifasciatum,* contained other species as well (Fig. 8c). In 1992, there were distinct differences in the seasonal patterns between the two shores for both groups (Fig. 8b, d). The three months of greatest *T. bifasciatum* recruitment on the north shore (June, July, and August) were the three months of lowest recruitment on the south shore. Thus, there appeared to be a distinct decoupling in the timing of recruitment between the two shores in 1992.

Variation in space: shores

In 1991, recruit abundance of *T. bifasciatum* was greater on the south shore than the north shore, although this difference was not significant (Fig. 4, Student's t test: $t = -1.0$, $P = 0.31$). The pattern in 1992 was opposite; the north shore had a significantly higher density of *T. bifasciatum* than the south shore (Fig. 4, Student's t test, $t = 2.9$, $P = 0.005$). For other species, recruit abundance was significantly greater on the north

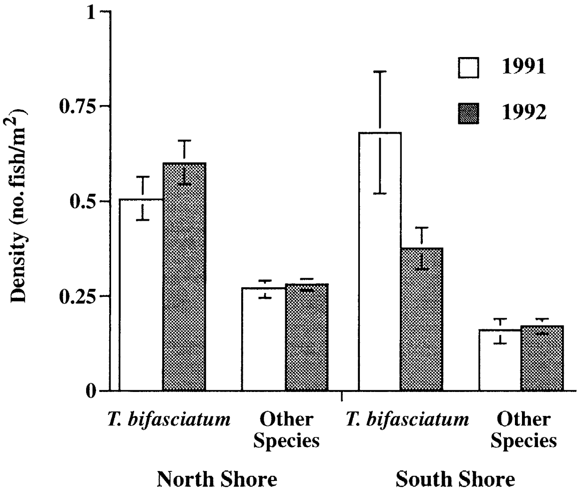

FIG. 4. Monthly recruit density (means ± 1 SE pooled over sites within the north and south shores) of *Thalassoma bifasciatum* and other fish species in 1991 and 1992.

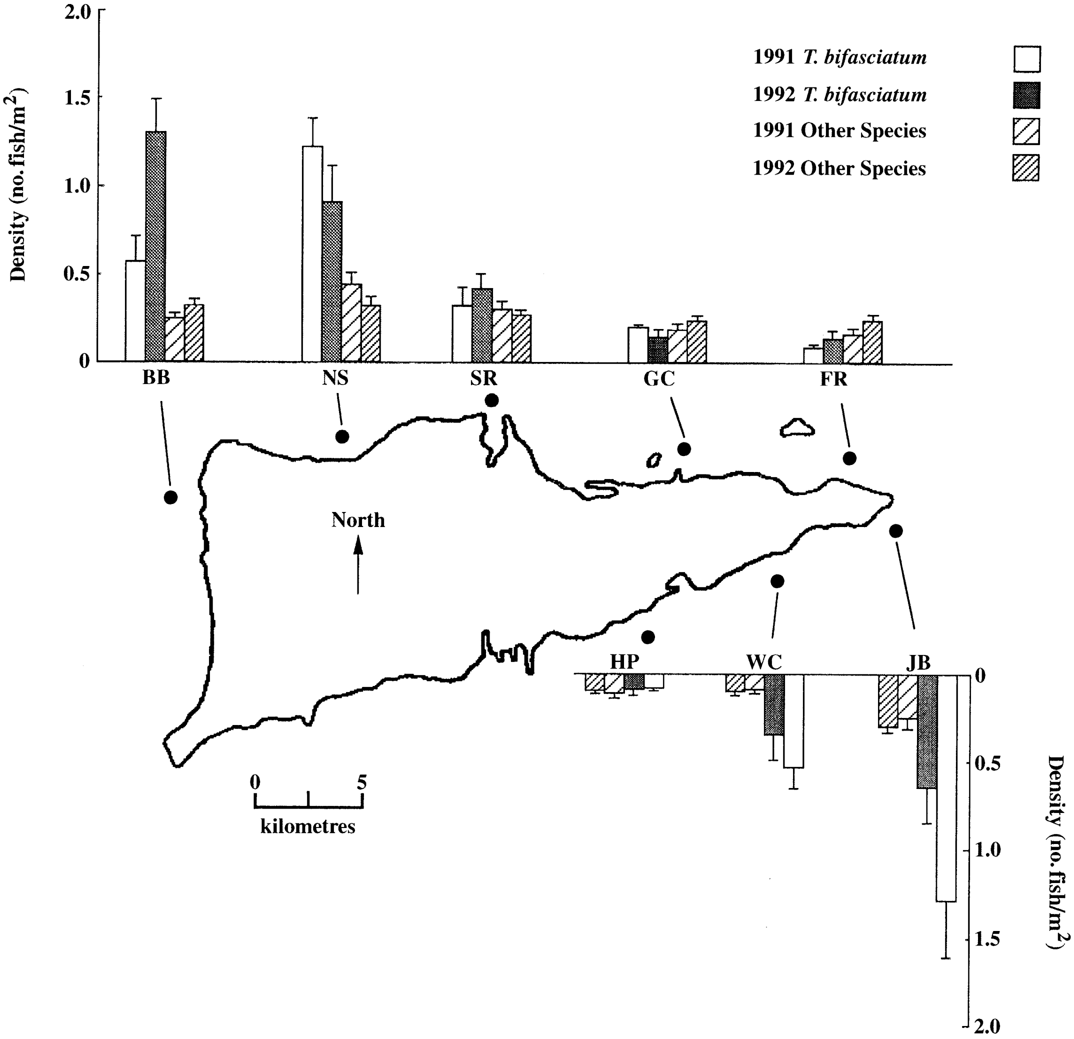

FIG. 5. Recruitment of *Thalassoma bifasciatum,* and of all other species, to sites around St. Croix. BB = Butler Bay; NS = Northstar; SR = Salt River; GC = Green Cay; FR = Forereef; HP = Ha'penny; WC = Wood Cottage; JB = Jacks Bay. Data show recruit density per month (means ± 1 SE).

shore than the south shore in both years (Fig. 4, Student's *t* test, 1991: $t = 2.5$, $P = 0.01$; 1992: $t = 4.4$, $P << 0.001$).

Variation in space: sites

Recruitment density of *T. bifasciatum* and other species differed significantly among sites within both the north and south shores (Tables 1b and 2b, Figs. 6 and 7). Furthermore, the distribution of recruits around St. Croix resulted in a striking pattern of gradients of density along the two shores. This pattern was most apparent for *T. bifasciatum* (Fig. 5). On the north or leeward shore, recruitment densities ranged from extremely low in the east to high in the west (Forereef = Green Cay < Salt River < Northstar = Butler Bay; Student-Newman-Keuls [SNK] test of differences in means from ANOVA in Table 1b). On the south shore, the pattern was reversed, with the highest recruitment reached at the easternmost site and densities decreasing towards the west (Jacks Bay > Wood Cottage = Ha'penny; SNK test of differences in means from ANOVA in Table 1b). When other species were examined, the general trend of greater recruitment in the west on the north shore and the east on the south shore was still present (Fig. 5), although the pattern was weaker. Comparisons of mean recruitment revealed that on the north shore the pattern was Northstar > Butler Bay = Salt River = Green Cay = Forereef (SNK test of differences in means from ANOVA in Table 2b). For the south shore, the settlement pattern was Jacks Bay > Wood Cottage = Ha'penny (SNK test of differences in means from ANOVA in Table 2b).

To test the significance of the observed density "gradients," the rankings of sites based on mean recruitment density per year were compared with their ranks based on distance from the eastern tip of the island for

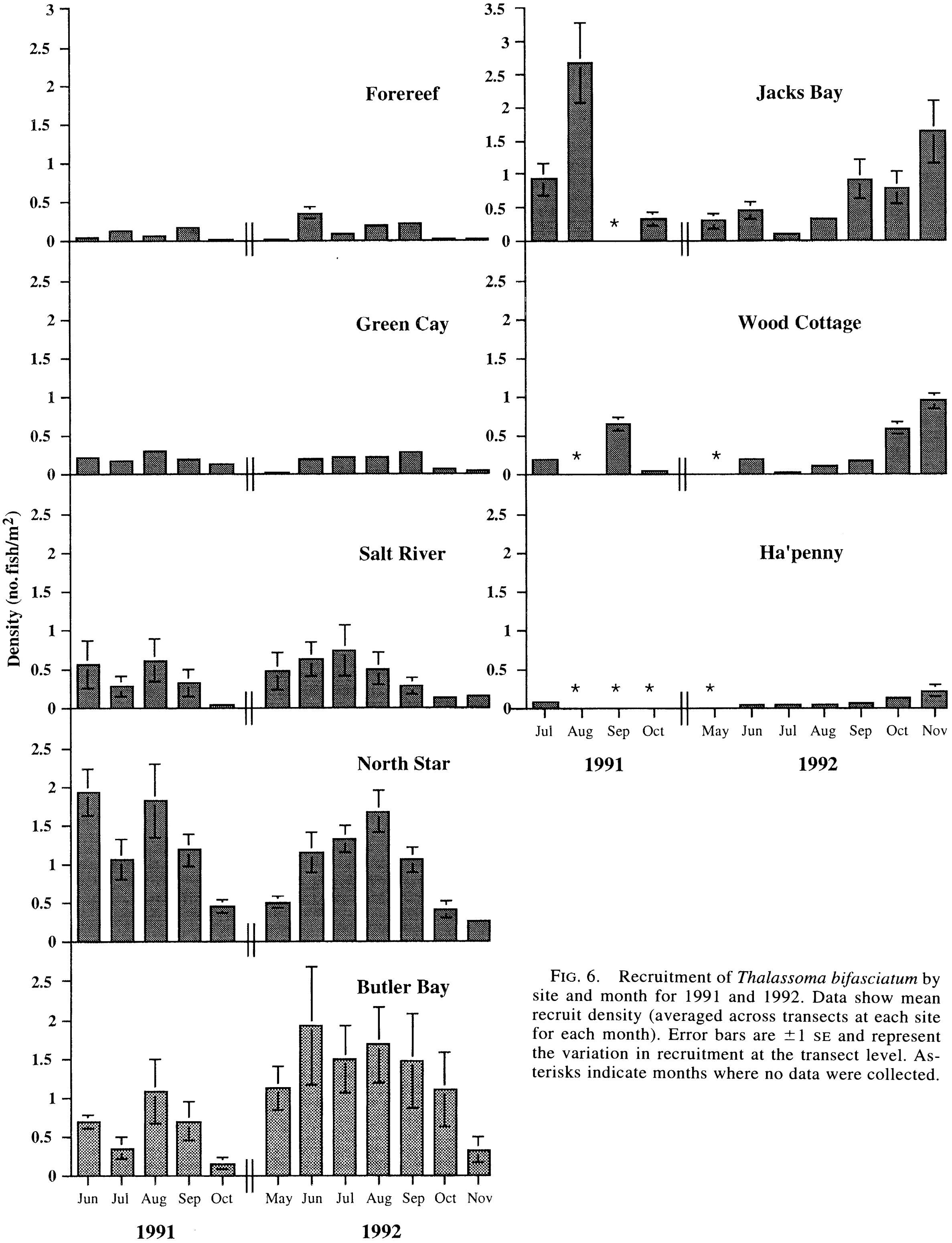

FIG. 6. Recruitment of *Thalassoma bifasciatum* by site and month for 1991 and 1992. Data show mean recruit density (averaged across transects at each site for each month). Error bars are ±1 SE and represent the variation in recruitment at the transect level. Asterisks indicate months where no data were collected.

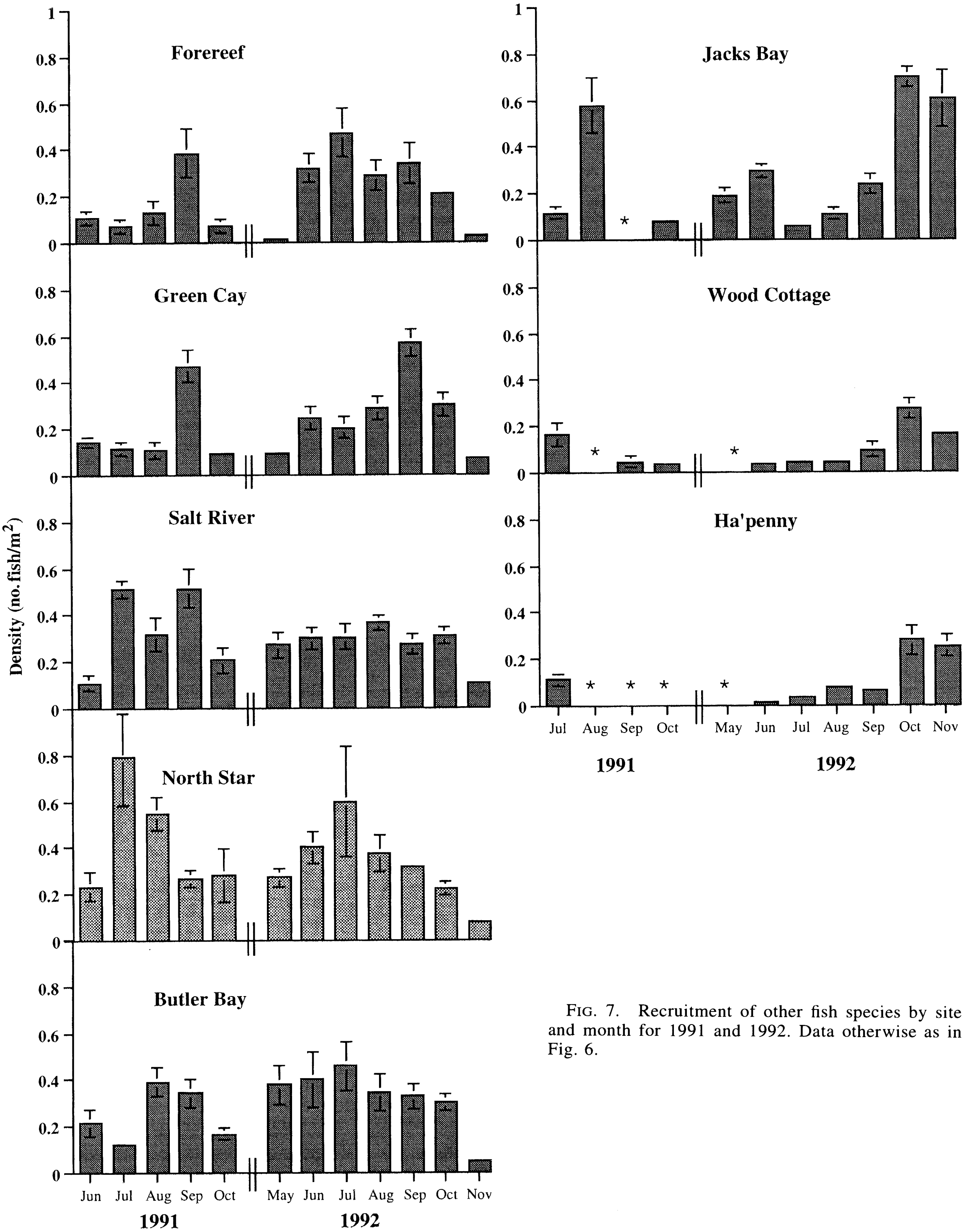

FIG. 7. Recruitment of other fish species by site and month for 1991 and 1992. Data otherwise as in Fig. 6.

the two shores separately. There was a significant positive correlation between recruitment of *T. bifasciatum* and distance from the eastern tip for the north shore in both 1991 and 1992, indicating that this pattern is a statistically significant "gradient" (Table 3). Because there were only three sites on the south shore, sample size precluded a statistical test. However, in both 1991 and 1992, the density of *T. bifasciatum* recruits was

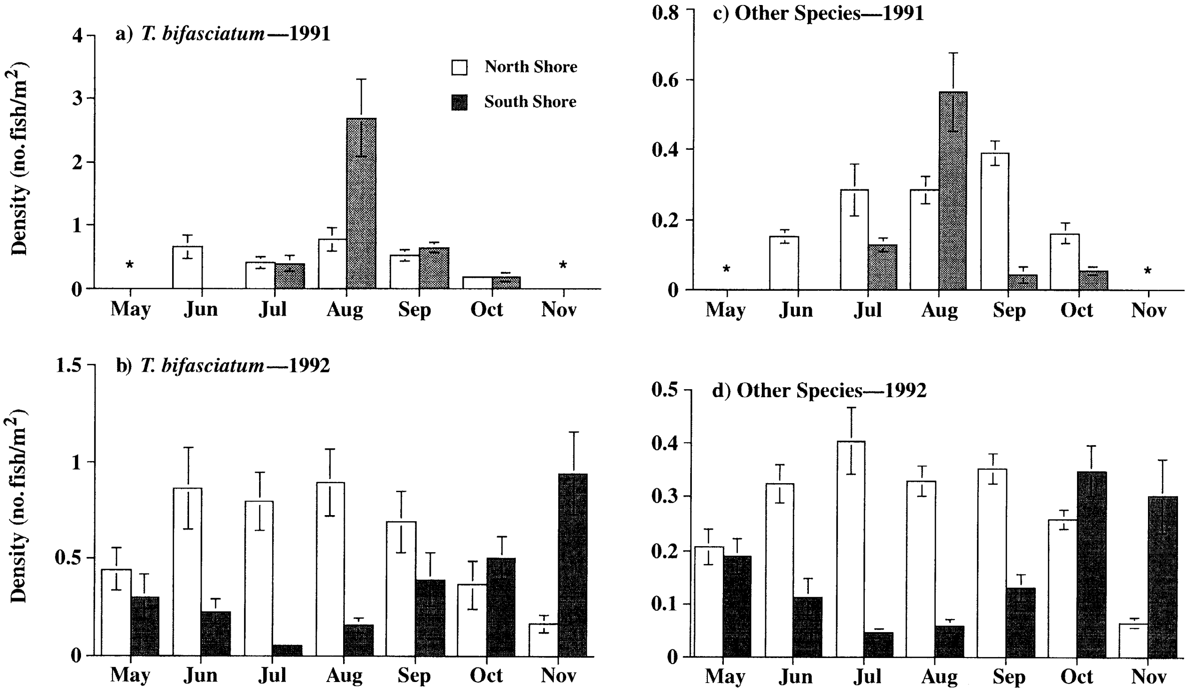

FIG. 8. Seasonal patterns of recruitment of *Thalassoma bifasciatum* (a, b) and other fish species (c, d) on the north and south shores of St. Croix in 1991 and 1992. Data are monthly recruit densities (means ± 1 SE pooled over sites within the north and south shores). Asterisks indicate months when no data were collected. Note differences in the scales of the y-axes.

highest at Jacks Bay (the easternmost site), intermediate at Wood Cottage (the middle site), and lowest at Ha'penny (the westernmost site; Fig. 5). For other species, the rank correlations between recruitment density at a site and position of the site along the shore were not significant in either year on the north shore (Table 3) and no statistical test was possible for the south shore sites. However, the trend in density for other species was similar to that observed for *T. bifasciatum* except on the north shore in 1992 (Fig. 5).

The observed spatial pattern of density gradients was repeated among monthly surveys (Figs. 6 and 7). The rankings of sites based on *T. bifasciatum* recruit density were concordant when compared among monthly censuses within each year on the north shore (Kendall's coefficient of concordance—1991: $W = 0.96$, $P < 0.001$; 1992: $W = 0.99$, $P < 0.001$). In addition, the mean yearly ranks were concordant between the two years (Kendall's coefficient of concordance: $W = 0.93$, $P < 0.001$). This statistical test was not possible for the south shore because of low sample size (three sites) but the rankings were also consistent (Fig. 6). Although there were distinct temporal (monthly and yearly) differences in the amount of recruitment to both shores and sites, coherence in ranks indicates that while absolute abundances changed over a season or year, the relative spatial distribution of recruits to sites remained constant. Rankings of sites for other species were not consistent over months within each year but mean yearly ranks were consistent between the two years (Kendall's coefficient of concordance—1991: $W = 0.17$, NS; 1992: $W = 0.42$, NS; (1991 + 1992): $W = 0.27$, $P < 0.05$).

TABLE 3. Results of Spearman rank-order correlations between recruitment density at a site and the position of that site down the shore for the north shore only, for both 1991 and 1992. (For south shore pattern see Fig. 5).

Year	Fish group	r_S	N
1991	*T. bifasciatum*	0.90*	5
1991	*T. bifasciatum*	1.0**	5
1992	Other species	0.70^{NS}	5
1992	Other species	0.75^{NS}	5

$^*P < 0.05$, $^{**}P < 0.01$, NS = $P > 0.05$.

Variation in space: transects

At the small (within-site) scale, there were significant differences for both species groups between transects at sites on the north shore (Tables 1b and 2b) and for *T. bifasciatum* on the south shore (Table 1b). Analysis of variance components showed that the variation among transects was generally less than the variation among sites (Tables 1b and 2b).

At most sites, the observed variation in recruitment of *T. bifasciatum* among transects was consistent both within each year and between the two years. Ranking transects in recruitment density over monthly censuses showed that within sites within each year, the distri-

TABLE 4. Concordance of the rankings of transects (within sites) in recruitment density of *Thalassoma bifasciatum* over months within each year of the study.

	W	
Site	1991	1992
Butler Bay	0.86**	0.55**
Northstar	0.64**	0.33*
Salt River	0.85**	0.73**
Green Cay	0.44$^{\mathrm{NS}}$	0.17$^{\mathrm{NS}}$
Forereef	0.69*	0.31*
Jacks Bay	0.74*	0.81**
Wood Cottage	0.43$^{\mathrm{NS}}$	0.22$^{\mathrm{NS}}$
Ha'penny	—	0.44*

Notes: W = Kendall's coefficient of concordance. A dash (—) indicates sample size too small for comparison.
$*P < 0.05$, $**P < 0.01$, NS = $P > 0.05$.

bution of recruits among transects was more consistent than would be expected if recruits were randomly distributed (Table 4). Only two sites, Green Cay on the north shore, and Wood Cottage on the south shore, showed temporal variability in rankings of transects. Interestingly, of all sites, these two had the lowest variation among transects in microhabitat features. The average density of *T. bifasciatum* recruits on transects in 1991 was significantly correlated with the average density on the same transects in 1992 ($r = 0.61$, $P = <0.0001$).

Importance of microhabitat to T. bifasciatum *recruitment*

Patterns of habitat distribution.—Although sites were chosen initially based on similar reef types, microhabitat features varied within each site. In addition, one-way ANOVA showed that several of the examined habitat characteristics varied significantly among sites around the island (Table 5). On the north shore, the mean depth and the percentage cover of living coral, dead coral, and large rubble all varied significantly among sites. On the south shore, the percentage cover of sand, pavement, large rubble, and small rubble varied significantly.

Small-scale analyses.—To determine the microhabitat preferences of newly settled *T. bifasciatum* at the small scale (transects), we used forward stepwise multiple regression. Average recruit density per transect was regressed against transect totals of all measured physical microhabitat characteristics (see *Methods: Physical habitat measurements*). To compare directly the amount of variation in recruitment to a particular transect explained by physical microhabitat characteristics vs. the amount of variation explained simply by the location of that transect on the island, a location term was included as an additional independent variable. Given the pattern of recruitment gradients along the shores of St. Croix, location for all transects at a particular site was the straight-line distance of that site from the east end of the island. The models were run separately on the data from the two shores.

TABLE 5. Summary of results of one-way analyses of variance of microhabitat characteristics at sites around St. Croix. Habitat data expressed as percent cover were arcsine transformed in all cases to meet the assumptions of homogeneity of variances.

	North shore		South shore	
Habitat feature	MS	F-ratio (df = 4, 23)	MS	F-ratio (df = 2, 12)
Living coral	0.022	25.45***	0.003	2.70$^{\mathrm{NS}}$
Sand	0.008	1.96$^{\mathrm{NS}}$	0.005	4.42*
Coral pavement	0.007	2.26$^{\mathrm{NS}}$	0.008	4.81*
Dead coral	0.024	34.82***	0.002	1.59$^{\mathrm{NS}}$
Large rubble	0.010	3.08*	0.024	11.63**
Small rubble	0.008	2.43$^{\mathrm{NS}}$	0.011	4.21*
Water depth	348.26	23.16***	10.40	2.52$^{\mathrm{NS}}$
Rugosity	0.484	0.46$^{\mathrm{NS}}$	1.263	0.84$^{\mathrm{NS}}$
Complexity	46.83	2.20$^{\mathrm{NS}}$	78.867	2.45$^{\mathrm{NS}}$

$*P < 0.05$, $**P < 0.01$, $***P < 0.001$, NS = $P > 0.05$.

Small-scale results.—Observations of newly settled *T. bifasciatum* showed that the fish were most common on pavement surfaces and were often clustered in or around small depressions or hiding under pieces of coral rubble. Recruits were seldom observed on open expanses of sand.

Recruit density on transects was significantly related to certain microhabitat features (Table 6). On the north shore, density of recruits per transect was negatively related to the amount of sand and positively related to the amount of pavement, large rubble, and complexity. On the south shore, recruitment was negatively related to depth and rugosity and positively related to complexity.

Large-scale analyses.—To investigate the role of

TABLE 6. Results of forward stepwise multiple regression analysis of habitat features explaining variance in recruitment of *Thalassoma bifasciatum* to transects on the north shore and south shore of St. Croix. Depth was log transformed to improve normality; habitat data expressed as percent cover were arcsine transformed.

	North shore		South shore	
Source	Partial r^2	P	Partial r^2	P
Distance	0.468	0.0001	0.62	0.001
Complexity	0.04	0.002	0.06	0.0003
Large rubble	0.04	0.05	—	—
Pavement	0.12	0.0003	—	—
Sand	0.15	0.05	—	—
Depth	—	—	0.17	0.003
Rugosity	—	—	0.07	0.02
Dead coral	—	—	—	—
Live coral	—	—	—	—
Small rubble	—	—	—	—
Model R^2	0.82		0.92	
Location on shore	0.468		0.62	
All habitat features	0.35		0.30	

Note: Dashes (—) indicate that the variable did not meet 0.05 significance level for inclusion in stepwise regression model.

TABLE 7. Spatial distribution of habitat variables along the two shores. Summary of simple linear regressions of each measured microhabitat feature vs. location of the site (distance in km from the eastern tip of St. Croix). Percent cover data (substrate characteristics) were arcsine transformed in all cases to homogenize variances.

	North shore		South shore	
Habitat feature	r^2	Relationship†	r^2	Relationship†
Living coral	0.47***	Positive	0.30*	Positive
Sand	0.21*	Positive	0.19^{NS}	—
Coral pavement	0.09^{NS}	—	0.09^{NS}	—
Dead coral	0.31**	Positive	0.20^{NS}	—
Large rubble	0.21*	Negative	0.16^{NS}	—
Small rubble	0.18*	Negative	0.08^{NS}	—
Water depth	0.38***	Positive	0.18^{NS}	—
Rugosity	0.001^{NS}	—	0.01^{NS}	—
Complexity	0.26**	Negative	0.05^{NS}	—

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, NS = $P > 0.05$.

† For both shores, a positive relationship means that variable increases from east to west and a negative relationship means that variable decreases from east to west. Dashes (—) indicate that there was no significant relationship.

habitat at the larger scale, we examined the relationship between recruitment and habitat at the scale of sites. This was done in two ways. First, using the small-scale regression results (Table 6) as a guide to the actual microhabitat preferences of the fish, we compared the island-wide pattern of physical characteristics important at the transect scale to the island-wide pattern of recruitment. We first determined, using simple linear regression, which habitat features were distributed in gradients along the two shores (Table 7). We then asked, for those characteristics that were important at the transect scale, was their pattern of distribution at the island-wide scale consistent with the island-wide pattern of recruitment (Table 8). Specifically, if a particular characteristic was positively related to recruitment at the transect scale, we asked whether there was greater recruitment to sites with greater amounts of that characteristic.

Second, to illustrate the pitfalls of conducting studies like this at only one spatial scale, we again used a correlative approach to determine which habitat characteristics were related to recruitment, but in this instance the analysis was performed at the scale of sites. We present results of forward stepwise multiple regressions of recruitment density per site on total microhabitat characteristics per site (effectively ignoring the relationship between recruits and habitat at the transect scale). This analysis represents the results we would have obtained had we only measured recruitment and habitat variability at the larger scale of sites.

Large-scale results.—Several habitat characteristics showed significant relationships with distance along the shore (Table 7). On the north shore, all measured characteristics except percent cover of coral pavement and rugosity were distributed in a significant gradient pattern, although the direction of the gradient varied. On the south shore, only the percent cover of living coral was distributed in a significant gradient pattern.

Although many features were distributed along the island in gradients, in no case did a characteristic that predicted recruitment to transects appear to be important at island-wide scale. On the north shore, no habitat characteristic that predicted recruitment at the transect scale had an island-wide distribution consistent with its being important at the large scale (Table 8). Pavement, which was preferred at the small scale, showed no relationship with distance along the shore. Sand, large rubble, and complexity were all distributed in gradients but in every case the direction was opposite to that predicted from recruitment patterns. On the south shore, there was no relationship between distance and any of the important small-scale features (depth,

TABLE 8. Predictions and results regarding the importance of habitat features at the island-wide scale.

Source	Relationship with density on transects	Predicted isle-wide pattern: Increasing from	Actual isle-wide pattern: Increasing from	Prediction met?
North shore				
Pavement	Positive	east to west	None	No
Sand	Negative	west to east	east to west	No
Large rubble	Positive	east to west	west to east	No
Complexity	Positive	east to west	west to east	No
South shore				
Complexity	Positive	west to east	None	No
Depth	Negative	east to west	None	No
Rugosity	Negative	east to west	None	No

Notes: On the north shore, recruitment was low in the east and increased towards the west (i.e., positive with distance; distance = 0 at the east end). On the south shore, recruitment was highest in the east and decreased towards the west (negative with distance). If features positively related to recruitment on a transect are important at the island-wide scale, their pattern of distribution on the island should match the pattern of distribution of recruits. Features negatively related to recruitment on a transect should have an island-wide distribution opposite to the pattern of recruitment.

rugosity, complexity) whether they were negatively or positively related to recruitment.

In our second analysis of site totals only, we found significant relationships between two features of the habitat and total recruitment to a site. On the north shore, recruitment was significantly and positively related only to the percentage cover of sand (stepwise multiple regression: model $r^2 = 0.48$, $F_{1,8} = 7.67$, $P < 0.05$). On the south shore, recruitment was significantly and negatively related only to the percentage cover of living coral (stepwise multiple regression: model $r^2 = 0.96$, $F_{1,4} = 100.65$, $P < 0.01$).

Large vs. small scale.—On both shores, the location of transects on the island (i.e., located within a site) explained more variation in recruitment to transects than all habitat characteristics combined (Table 6). Distance along the north shore explained 47% of the variation, compared with 35% explained by all habitat features combined. On the south shore, distance explained 62% of the variance compared with 30% explained by habitat.

DISCUSSION

Spatial and temporal variation

In this study, the spatial component to recruitment variability was far more pronounced than the temporal component. On the island as a whole, there was a 12-fold difference in recruitment density of *Thalassoma bifasciatum* (averaged over both years) between the sites of highest and lowest recruitment but no difference in recruitment density (averaged over all sites) from 1991 to 1992. Although recruitment was variable at all spatial scales studied, the spatial pattern of distribution of recruits was consistent at both the site and transect scales within and between years. The main temporal changes occurred within years (i.e., seasonal changes in abundance). In addition, both the spatial distribution of recruits, the overall density, and the patterns of seasonal change were markedly different between the leeward and windward shores of the island.

Although variability in recruitment of coral reef fishes has been well documented (for review see Doherty and Williams 1988, Doherty 1991), few studies have found consistency in spatial patterns of recruit abundance over time, especially at smaller spatial scales (but see Williams 1986, Victor 1986, Fowler et al. 1992). A more common finding has been large interannual variation in both abundance and distribution of recruitment (Eckert 1984, Sale et al. 1984, Shulman 1985, Doherty 1987, Walsh 1987, Fowler et al. 1992). In St. Croix, there was little evidence of interannual variability in mean yearly abundance or distribution within shores (among sites) or within sites (among transects). Although the three sites with the greatest average yearly densities (Butler Bay, Northstar, and Jacks Bay) showed some interannual differences in average density or switching of ranks relative to one another, these differences were not large enough to obscure the temporal consistency of the island-wide pattern of distribution.

In order to make meaningful conclusions about year-to-year stability in population numbers, studies must be conducted at time scales appropriate to the lifespans of the organisms. In the present study, monthly recruitment monitoring took place for only 2 yr. Although this period of monitoring may be appropriate for *T. bifasciatum,* which lives ≈2–3 yr, many other coral reef fishes may live much longer. We did, however, conduct additional censuses on an intermittent basis at several sites around St. Croix in both 1990 and 1993. Although these data are too temporally sparse to allow comparisons of seasonal patterns of recruit distribution or abundance, we were able to assess the large-scale patterns of distribution. The island-wide distribution was similar in these years to the patterns presented for 1991 and 1992 (J. E. Caselle, *unpublished data*). Thus, it appeared that the processes resulting in the large-scale distribution of recruits around St. Croix were consistent over at least 4 yr. Although stability at this temporal scale may have important consequences to the population dynamics of shorter-lived organisms, longer time series may be necessary to understand processes affecting populations of longer-lived organisms. Other potentially important physical or biological oceanographic processes affecting recruitment will only be understood by investigating longer time series than in this study.

In St. Croix, both the overall abundance of recruits and the large-scale patterns of distribution were different on the two shores. In general, recruit densities were greater on the north or leeward shore. The only notable exception to this pattern was a very large pulse of recruitment on the south shore in August 1991.

The most striking result was not in terms of overall abundance on the two shores, but in distributional patterns. Although both shores showed spatial density gradients, the directions of the gradients were opposing. On the leeward shore, recruitment density ranged from low to high in a direction from east to west. On the windward shore, recruitment ranged from high to low in the same direction. This distributional pattern was temporally consistent on both shores at all temporal scales investigated. Despite temporal changes affecting the absolute abundance of recruitment to a site, the relative abundances among sites remained similar.

Although recruitment variability has been well documented at many scales, this is one of few studies of reef fishes of which we are aware that consistently monitored recruitment around an island, allowing comparisons between windward and leeward shores. Hawkins and Hartnoll (1982) measured settlement of barnacles on two shores of the Isle of Man. At both sites they found a positive relationship of settlement density with onshore winds and the strength of that relationship differed between the two shores. The relationship was stronger on the side with the semiprotected bay site (Port Erin) than on the side with more open shores (Port St. Mary). There are other fundamental environmental differences between exposed and protected shores that can affect settling larvae either indirectly or directly. Storms, waves, and sediment transport may differentially affect the physical structure of the reef, resulting in shore-to-shore variation in the amount of suitable habitat. Other properties of water flow such as turbulence and velocity may directly affect both delivery rates and settling behavior of larvae, in addition to affecting reef structure. Indeed, there are measurable habitat differences between reefs on the north and south shores of St. Croix (See Adey 1975 for complete description of St. Croix reefs). However, these substrate differences did not appear to explain the between-shore patterns of recruitment.

The seasonal patterns indicated that the processes affecting successful recruitment were not acting at the same times on the two shores. This was most noticeable in 1992 when the seasonal patterns were markedly different on the leeward and windward shores. The timing of maximum recruitment was completely offset: recruitment peaked in the summer months on the north shore and the fall months on the south shore. In 1991, the seasonal patterns of recruitment were similar on the two shores with the exception of the extremely large pulse of recruitment in August that occurred only on the south shore. Although recruitment to the north shore also reached its maximum in August, there was no evidence of a pulse of the magnitude observed on the south shore. Seasonality in recruitment of coral reef fishes is common (Luckhurst and Luckhurst 1977, Walsh 1987). However, to our knowledge, large differences in seasonal patterns of recruitment of a single species, such as seen in this study in 1992, have not been documented at such small spatial scales as the windward and leeward shores of a single island. Differences of this magnitude are more typically associated with widely separated geographic areas.

The differences in distribution, magnitude, and timing of recruitment between the leeward and windward shores of St. Croix suggested that the process or processes determining recruitment were oceanographic in nature and acted at scales smaller than the island of St. Croix. In contrast, within each shore, the spatial patterns of recruitment were consistent over time, indicating that the difference between shores was not due to random processes. Temporal consistency in recruitment patterns to natural habitats is often indicative of deterministic processes such as habitat choice (Doherty 1987) but may be difficult to distinguish from consistent larval delivery. What are the potential processes that determine the spatial distribution of recruits within sites, among sites on shores, and between shores?

Causes of spatial variation: habitat or larval availability?

Since recruitment generally varied more in space than time in St. Croix, we focused on the processes affecting the spatial distribution of recruits. Variation in recruitment at any spatial scale is due to one or more of the following processes: (a) differential delivery of larvae, (b) differential settlement on preferred habitat, (c) early post-settlement movement to preferred habitat, or (d) differential early post-settlement mortality. In this study, we attempted to distinguish between physical processes determining larval delivery and habitat selection at or just after settlement by searching for correlations between densities of recently settled fish and features of the habitat at large and small spatial scales. It is important to note that we did not directly measure larval availability; instead we used recruitment as an indicator of availability. We discuss the potential problems with this approach below.

Many previous studies identify a spatial scale or scales at which recruitment variation is coherent over time, and then infer from the coherence of pattern which processes might be acting at those scales (e.g., Williams 1986, Fowler et al. 1992). The assumption inherent in this procedure is that some processes are more likely to result in consistent patterns over time than others. For example, it is often assumed that oceanographic processes affecting larval delivery are likely to act in a stochastic manner that will result in temporal variation in recruitment (Choat et al. 1988). Other processes, such as habitat selection, are assumed to act more deterministically, resulting in spatial variability that is consistent over time. In actuality, there is little real information about the spatial scales over which particular processes are likely to act. Without directly quantifying the effects of actual processes at varying scales, care must be taken in making inferences about the stochastic or deterministic nature of a process.

In St. Croix, the distributional patterns of recruits were consistent from year to year at two spatial scales—sites and transects. What processes produced these consistent patterns? Were they the same at the different spatial scales?

When measuring recruitment variability on natural habitat, it is difficult to separate the effect of larval availability from that of habitat selection at settlement (Doherty 1991). For coral reef fishes, little is known about the maximum spatial scale over which larvae or new recruits may choose habitats, and we are equally ignorant about the minimum spatial scale over which physical forcing may be important (but see Butman 1987 for invertebrates). Given the consistent spatial patterns of recruitment at both scales, one might predict that habitat (which changed little over the course of the study) was important at both scales. Microhabitat availability did indeed appear to be quite important at the smaller scale since certain transects within each site consistently received more recruitment than others, and those transects had distinct microhabitat features associated with them. Although it is possible that larvae are differentially delivered to transects by fine-scale hydrographic processes (Butman 1987, Hamner and Wolanski 1988, Mullineaux and Butman 1990, Butman et al. 1992), the fact that recruitment per transect was significantly related to certain features of the habitat throughout St. Croix argues against this possibility. Overall, microhabitat features explained a large amount (30–35%) of variance in recruitment to transects. Although we could not distinguish between differential settlement, very early post-settlement movement, and very early post-settlement mortality in this study, none of these processes is inconsistent with the hypothesis that habitat affects recruitment to a transect (Jones 1984).

Given the apparent importance of habitat to small-scale variation in recruitment density, how important is habitat at the large scale? We first tested the importance of habitat at the large scale by using the small-scale results as a guide. We assumed that larvae or new recruits were more likely to be able to choose habitat at the transect scale and thus we compared the patterns of distribution of preferred and avoided habitat features (at the transect scale) with the distribution of recruits among sites. In every case there was either no relationship between recruitment and habitat, or a relationship that was opposite to the prediction. For example, on the north shore, recruits were rare on transects composed of large amounts of open sand. Yet the sites with the highest percentage cover of sand also had the highest recruitment densities. Given the temporal stability of the patterns (i.e., recruitment was consistently greater at those sandy sites), and in the absence of smaller-scale data, we might have concluded that habitat was important at that scale. We tested this directly by ignoring all data collected at the small scale and analyzing site totals only. As this analysis demonstrated, if we had conducted our study only at the larger scale, and had neglected the smaller-scale variability, we might have concluded that sand was important to *T. bifasciatum* recruitment. Although this example is extreme because we know that *T. bifasciatum* recruits were rarely found on open sand, it highlights the need to sample at scales appropriate to the size and behavior of the organism being studied. It is probable that one will find correlations between habitat features and recruitment at any spatial scale. However, these correlations may result from a covariance between oceanographic processes that may affect the transport of larvae and habitat features. Returning to our example of greatest recruitment to sites with high percentage cover of sand, that correlation may in fact be a result of the same oceanographic features delivering both sand and larvae. We concluded that at the scale of sites along the island, habitat was not a primary cause of the patterns of distribution. Instead, it appears that physical transport processes were more important determinants of the spatial patterns of recruitment along the two shores of St. Croix. Furthermore, covariance between physical processes and habitat structure can easily lead to false conclusions about the role of various processes in determining patterns of recruitment at different spatial scales.

Possible hydrographic explanations for the unique large-scale spatial patterns

If physical transport is important, can we explain the curious distributional patterns observed on the two shores? The nearshore physical oceanography around St. Croix is likely to be complex and at this point, is quite unknown. Although most marine ecologists would agree that understanding variability in recruitment of marine organisms will require understanding of the interaction of various physical processes at a variety of scales, collaborative efforts between oceanographers and marine ecologists are still needed. We know that tidal range on St. Croix is small and both shelf and coastal currents are primarily driven by winds and waves (Hubbard 1989). In general, the prevailing winds are east-to-west trade winds. During the times of year in which this study took place, longshore currents on St. Croix tend to run east to west. One possibility is that these large scale spatial patterns are simply due to residual flow past the island.

In a scenario of residual flow moving larvae past the island, the distribution of recruits on the south shore would be consistent with a model of patch depletion or downstream filtering (Victor 1984, Gaines et al. 1985). Densities of newly settled fishes are highest at the upstream end of the south shore and lower downcurrent. Patchiness in larval distributions is well established; a number of workers have directly or indirectly identified the presence of patches of fish larvae (Victor 1984, Williams 1986, Doherty 1987, Kingsford and Choat 1989, Williams and English 1992, Cowen and Castro 1994). By observing patterns of recruitment of fishes to reefs in Panama, Victor (1984) hypothesized that larvae travel in a patch or front from which settlement occurs. From the coherence of recruitment pulses over his entire sampling area, he was able to estimate the size of patches to be >46 km. One interesting possibility is that patches or fronts of larvae are transported on the prevailing currents and move east to west along the south shore of St. Croix. Settlement from the front would occur when the front first neared reef habitat, resulting in greater settlement upstream and lower settlement downstream as the front became depleted of larvae. This hypothesis requires that patches of larvae collide with the island from due east or northeast.

However, the distribution of recruits on the north shore is exactly opposite to the patterns predicted for downstream filtering, since densities were low upstream and high downstream. Given the decoupling in seasonal patterns seen in 1992 between the two shores, perhaps an entirely different feature or features was responsible for the pattern on this shore. One possibility is tidal forcing. In a similar study in Barbados, Sponaugle (1994) found that tidal forcing influenced patterns of settlement of reef fishes along a leeward shore. Another possibility is retention in an eddy or convergence area. Preliminary data indicate that just offshore of the Salt River site is an area of converging and slowed currents and high reef fish larval densities (R. K. Cowen, *unpublished data*). Thus the high recruitment densities observed on the northwestern shore may be a result of high larval availability. Eddy generation in the lee of islands has been well documented and modeled (Hamner and Hauri 1977, Alldredge and Hamner 1980, Wolanski et al. 1984) and features including eddies have been shown to retain pre-settlement fishes near reefs (Kingsford and Choat 1989, Boehlert et al. 1992). The operation of such a mechanism in St. Croix requires further investigation.

Thus, the possibility exists that two or more distinct oceanographic processes may be important in the delivery of reef fish larvae to sites on a single island. If true, one possible outcome is that there may be multiple sources of reef fish larvae to St. Croix. If the south shore pattern was due to drift via prevailing currents then larvae may have been delivered from upstream islands. If on the north shore a local process was retaining larvae, then all or some fraction of those retained may have been locally produced. We stress that this possibility remains to be investigated further. If it was operating, there are important implications for reef fish management schemes. Some local populations may be completely open and dependent on distant sources of supply, while nearby populations of the same species may be much more closed and dependent on local production. Understanding the relative "openness" of marine populations is a critical area for future studies of marine ecology.

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