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Ivan Mateo

USVI Division of Fish and Wildlife

William J. Tobias

USVI Division of Fish and Wildlife

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A COMPARISON OF FISH ASSEMBLAGES AMONG FIVE HABITAT TYPES WITHIN A CARIBBEAN LAGOONAL SYSTEM

Ivan Mateo¹ and William J. Tobias

USVI Division of Fish and Wildlife, Rainbow Plaza 45 Marshall, Fredericksted, St Croix USVI 00840

¹Current Address. Department of Fisheries, Animal and Veterinary Science, University of Rhode Island, Kingston, RI 02881 USA. Phone (401) 398-1742, Fax (401) 398-1742, E-mail imateo32@hotmail.com.

ABSTRACT Fish assemblages associated with patch reefs, rubble, seagrass, algal plain, and sandy habitats types were studied at St Croix's Southeastern barrier reef lagoon using underwater visual census techniques. Higher species richness and fish density were observed over patch reefs/rubble habitat followed by seagrass, algal plain, and unvegetated sandy habitat types. *Thalassoma bifasciatum*, *Haemulon flavolineatum*, and *Acanthurus chirurgus* were the most common fishes in highly structured habitat types (patch reef, rubble). *Halichoeres bivittatus*, *Sparisoma radians*, newly settled grunts (i.e., *Haemulon* spp.), and juveniles of *Ocyurus chrysurus* were mainly associated with vegetated habitat types (seagrass, algal beds), while *Xyrichtys martinicensis* and *Coryphopterus glaucofraenum* were common over unvegetated sandy habitat types. Cluster analysis among backreef lagoon habitat types based on the entire fish density data showed distinct associations of fish assemblages by habitat type, regardless of season. Fish assemblages in the more structured habitat types were similar to each other but different from unstructured vegetated, and unvegetated habitat types. These results suggest that differences in fish species richness and density in the backreef lagoon are related to habitat type. The ecological importance and need for protection of backreef lagoon habitat types are discussed in relation to their potential role as nurseries for many fish species.

INTRODUCTION

Nearshore ecosystems such as seagrass meadows, marshes, and mangrove lagoons supply many vital ecological functions in coastal waters, including shoreline protection, and nutrient cycling (Ogden and Gladfelter 1983, Parrish 1989). Most notably, these ecosystems provide food and refuge that supports a great abundance and diversity of fishes as well as shrimp, oysters, crabs, and other invertebrates (Ogden and Ziemann 1977, Shulman 1984, Shulman 1985, Parrish 1989). In the Caribbean, it has generally been accepted that mangroves and seagrass meadows form important nurseries for juveniles of several reef fish species (Ogden and Gladfelter 1983, Parrish 1989, Nagelkerken et al. 2000), and juvenile coral reef fishes have been frequently observed in mangroves and seagrass meadows in the Caribbean (e.g., Baelde 1990, Sedberry and Carter 1993, Appeldoorn et al. 1997, Lindeman et al. 1998, Nagelkerken et al. 2000). The adults of these species have been observed on reef environments or in offshore waters, suggesting the migration of juvenile from the mangroves and seagrass beds to the reef or deeper waters at a certain age (Ogden and Ehrlich 1977, Weinstein and Heck 1979, Rooker and Dennis 1991, Appeldoorn et al. 1997, Lindeman et al. 1998, Nagelkerken et al. 2000). Although numerous studies have been done on mangrove, seagrass, and coral reef systems, only recently researchers have investigated the connectivity among these coastal ecosystems (Sedberry and Carter 1993, Nagelkerken et al.

2000, Adams and Ebersole 2002). Comparisons of nursery value among nearshore habitat types have usually focused on a single habitat (i.e., mangrove or seagrass) (Robblee and Zieman 1984, Baelde 1990, Rooker and Dennis 1991) even though individual species may use many different habitats. Furthermore, embayments and lagoons often not only contain mangroves and seagrass meadows, but a variety of other shallow-water habitats like algal plains, areas with bare sediment, sand-rubble zones, or patch reefs. Seagrass meadows and mangroves may be less important as nurseries in regions where animals use alternative habitats successfully. Few studies have quantified the proportions of reef fishes that pass through these nursery habitats, and information concerning other habitats that can be used as alternative nurseries are lacking. Thus, linkages of fishes between these backreef lagoon habitats remain largely unknown (Ogden and Gladfelter 1983, Birkeland 1985, Parrish 1989). Therefore, this study addresses the following questions: 1) Does species composition and abundance differ among backreef lagoon habitat types? 2) Which habitat types are used as nurseries by selected fish species? 3) Which backreef lagoon habitat types are utilized more by a fish species when multiple nursery habitat types are present? 4) Do fish species show an ontogenetic shift from nursery habitat types to other backreef lagoon habitat types? 5) Do closely related fish species show similar seasonal patterns in habitat use?

Figure 1. Location of the southeastern backreef lagoon of St. Croix, USVI. The 3 embayments studied, Great Pond Bay (GPB), Robin Bay (RB) and Turner Hole Bay (THB) are shown.

MATERIALS AND METHODS

The nearshore nursery habitat types in 3 protected backreef lagoon embayments on St. Croix's southeast coast (Turner Hole Bay, Robin Bay and Great Pond Bay) (Figure 1) were sampled monthly from July 2000 to July 2001. For each bay, a 20 m x 20 m grid pattern was laid over a nautical chart. Grid intersecting points were labeled with consecutive numbers and were the basis for selecting transect starting points for each embayment. The number of starting points surveyed (10 in each of the 3 embayments) was based on a preliminary fish census (Rogers et al. 1994), and each starting point was selected randomly each month. At each of the 10 starting points, a single 50 m transect line (marked at 1 cm intervals) was laid out on a compass bearing randomly selected for each transect. At each starting point, one weighted end of the 50 m transect line tape was dropped and was laid by a diver in the direction of the compass bearing. On each transect, 100 m² were surveyed visually for fish, with 2 parallel 1 m x 50 m belt transects surveyed by 2 divers swimming on opposite sides of the transect line.

At each transect site, a fish census and a benthic survey was done. Each diver recorded fish species and size class of individuals for each species and size class. Fish size classes were characterized as < 5 cm, 5–10 cm, and > 10 cm in total length (TL). For most species, juveniles ≤ 5 cm were recorded as recruits. For smaller species,

such as wrasses, grunts, and damselfishes, juveniles ≤ 3 cm were considered as recruits. Larger individuals in size classes 5–10 cm and > 10 cm were considered as sub-adults. To minimize the potential bias of counting the same individual twice along the belt transect, divers conferred with each other using hand signals to make sure fish were counted only once (Eberhardt 1978), and divers were trained to maintain constant swimming speed along the transect, and not to count fish that entered the census area after the visual census had started (Samoylis and Carlos 2000).

For the benthic survey, each diver recorded the dominant habitat type at the beginning and end of changes in habitat type (to the nearest cm) under the transect line. Five benthic habitat types were identified:

Patch reef: isolated, high calcareous structure (not part of the contiguous reef) with a vertical profile that often, but not always, contained live coral cover.

Rubble: low-relief calcareous structure composed primarily of dead/dying coral fragments that were not attached to the habitat type.

Sand: areas of open sand with little (<10% cover) or no plants or coralline material, mostly unvegetated.

Algal plain: sandy bottom dominated by (>60% cover) *Dictyota* spp., *Halimeda* spp., *Penicillus* spp., *Acanthophora* spp., and/or *Udotea* spp., which may have include sparse stands of *Syringodium filiforme* and *Thalassia testudinum*.

Figure 2. Plot of the total percent of habitat cover found on southeastern barrier reef lagoons in St Croix when all bays were pooled. Number of samples per habitat $N = 24$. Total area surveyed = 70,000 m²

Seagrass: monospecific or nearly monospecific stands of, with varying densities of *S. filiforme*.

Percent cover of each habitat type was estimated from linear coverage along belt transects. The proportional composition of each habitat type covered in each belt transect was estimated by measuring the length of line overlying each habitat type and dividing it by the total length of the transect.

Prior to conducting data analyses, fish density estimates from both divers were checked for independence with a Pearson product-moment correlation coefficient. This was used to test for independence between the paired diver observations (Zar 1984). If uncorrelated, the paired transects could be used as potentially independent samples. We considered $r < 0.50$ to indicate independence. Correlation between paired divers was low ($r = 0.43$, $P = 0.343$, $n = 330$), and we interpreted the data generated from the 2 divers as separate and independent census data sets.

Data were standardized by month by pooling belt transects of all 3 embayments by habitat type. This allowed for equal sample size ($N = 24$) for the one year study. Monthly data were further pooled into winter (December, January, February), spring (March, April, May), summer (June, July, August), and fall (September, October, November) seasons. The seasonal grouping was based on previous temperature measurements done by the USVI Division Fish and Wildlife.

Normality of the number of fish per transect, number of species per transect, size class distribution, and fish density of the most abundant species were verified with the Kolmogorov-Lilliefors Normality test (Zar 1984). Since the estimates failed the normality test even after $\log_{10}(x + 1)$ or square root transformation, non-parametric statistics were used to analyze the data. Overall fish density, species richness, density of the most abundant

species recorded on transects within habitat type, density of economically important species among habitat types and size classes were examined with two-way ANOVA on ranks (Sokal and Rohlf 1981) unless specified. If the overall F-value was significant, Tukey's pair-wise multiple comparison procedure was used to separate mean values. Finally, fish density delineated by habitat type, season and bay were analyzed using the Bray-Curtis similarity measure (Krebs 1999) and clustered using the average linkage method with the PRIMER software package (Plymouth Marine Laboratories, UK).

RESULTS

Species composition among habitat types

Seventy-one fish species were recorded within the St. Croix southeastern backreef lagoonal system. The estimated percent cover of backreef lagoon habitat types pooled by bay was dominated by seagrass and sand, whereas patch-reef and rubble covered the least area of the bottom (Figure 2). Species richness was highest on patch reef (54), followed by rubble (41) and seagrass beds (39) habitats (Table 1), and lowest on algal beds (28) and sandy habitats (10). Thirty-five species occurred over both patch reef and rubble habitats, while the overlap in species between seagrass and the other habitat types was low (Table 1). The most abundant taxa per habitat type were:

Patch reef: *Thalassoma bifasciatum*, *Haemulon flavolineatum*, *Halichoeres bivittatus*, *Acanthurus chirurgus*, and newly settled grunts (*Haemulon* spp.), which all together made up 56% of the total number of fishes recorded from the patch reef habitats.

Rubble: newly settled grunts (*Haemulon* spp.), *H. bivittatus*, *A. chirurgus*, *S. leucostictus* and *T. bifasciatum*, which together made up 76% of the total number of individuals at this habitat type.

Seagrass: newly settled grunts (*Haemulon* spp.), *Sparisoma radians*, *H. bivittatus*, *H. flavolineatum*, and *A. chirurgus*. Those species comprised 90.0% of the total fishes recorded in the seagrass beds.

Algal plain: newly settled grunts (*Haemulon* spp.), *H. bivittatus*, *H. flavolineatum*, *S. radians*, and *A. chirurgus*, which made up 96% of the total number of individuals.

Sand: newly settled grunts (*Haemulon* spp.), *Xyrichtys martinicensis*, *Caranx ruber*, *H. bivittatus*, and *Coryphopterus glaucofraenum*. Those species comprised 98.0% of the fishes recorded in sandy habitats.

Variation in species richness

Species richness differed significantly among habitat types (ANOVA, $P < 0.001$, $df = 4, 20$) but not among sea-

TABLE 1

Fish species abundance on nearshore habitat types in a tropical lagoon in southeastern coast of St. Croix, USVI.

Species	Patch Reef	Rubble	Seagrass	Algal Plain	Sand	Total
<i>Haemulon</i> spp.	337	646	2599	3824	256	7662
<i>Halichoeres bivittatus</i>	406	318	615	241	27	1607
<i>Sparisoma radians</i>	39	71	758	53	0	921
<i>Haemulon flavolineatum</i>	446	59	248	156	0	909
<i>Acanthurus chirurgus</i>	383	134	139	6	1	663
<i>Thalassoma bifasciatum</i>	464	117	21	0	0	602
<i>Stegastes leucostictus</i>	349	144	31	5	0	529
<i>Acanthurus bahianus</i>	210	144	84	36	0	474
<i>Scarus iseri</i>	224	78	21	10	0	333
<i>Stegastes partitus</i>	164	44	3	0	0	211
<i>Xyrichtys martinicensis</i>	11	0	29	25	134	199
<i>Ocyurus chrysurus</i>	31	5	76	28	0	140
<i>Lutjanus mahogoni</i>	25	32	44	17	0	118
<i>Haemulon plumieri</i>	78	2	20	16	0	116
<i>Pseudupeneus maculatus</i>	12	7	71	0	0	90
<i>Cryptotomus roseus</i>	0	0	55	22	4	80
<i>Sparisoma viride</i>	54	22	0	0	0	76
<i>Holocentrus adscensionis</i>	62	8	0	0	0	70
<i>Stegastes adustus</i>	51	8	0	0	0	59
<i>Sphoeroides spengleri</i>	7	4	17	28	0	56
<i>Halichoeres poeyi</i>	4	1	45	5	0	55
<i>Canthigaster rostrata</i>	26	4	8	7	0	45
<i>Acanthurus coeruleus</i>	24	3	14	0	0	41
<i>Caranx ruber</i>	4	0	7	1	28	40
<i>Epinephelus guttatus</i>	32	7	0	0	0	39
<i>Sparisoma chrysopteron</i>	25	9	0	0	0	34
<i>Sparisoma aurofrenatum</i>	32	4	0	0	0	36
<i>Chaetodon striatus</i>	4	11	2	10	0	27
<i>Cephalopholis fulva</i>	17	10	0	0	0	27
<i>Myripristis jacobus</i>	24	0	2	0	0	26
<i>Coryphopterus glaucofraenum</i>	0	17	0	0	9	26
<i>Monacanthus ciliatus</i>	0	1	16	2	0	19
<i>Abudefduf saxatilis</i>	14	1	0	0	0	15
<i>Chromis multilineata</i>	13	2	0	0	0	15
<i>Holocanthus ciliaris</i>	12	0	1	1	0	14
<i>Microspathodon chrysurus</i>	8	4	0	0	0	12
<i>Halichoeres radians</i>	10	2	0	0	0	12
<i>Caranx crysos</i>	0	0	7	4	0	11
<i>Chaetodon capistratus</i>	7	1	2	0	0	10
<i>Pareques acuminatus</i>	10	0	0	0	0	10
<i>Stegastes planifrons</i>	6	4	0	0	0	10
<i>Stegastes variabilis</i>	3	6	0	0	0	9
<i>Xyrichtys splendens</i>	0	0	3	3	1	7
<i>Apogon</i> spp.	2	2	0	2	0	6
<i>Serranus tigrinus</i>	5	1	0	0	0	6
<i>Paralichthys tropicus</i>	0	0	3	1	1	5

TABLE 1 (cont.)

Fish species abundance within nearshore habitat types in a tropical lagoon in southeastern coast of St. Croix, USVI.

Species	Patch Reef	Rubble	Seagrass	Algal Plain	Sand	Total
<i>Balistes vetula</i>	3	2	0	0	0	5
<i>Sphyraena barracuda</i>	0	0	4	0	0	4
<i>Lutjanus synagris</i>	1	0	2	1	0	4
<i>Lactophrys triqueter</i>	0	0	1	1	2	4
<i>Chromis cyanea</i>	3	0	0	0	0	3
<i>Aulostomus maculatus</i>	0	0	2	0	0	2
<i>Calamus bajonado</i>	0	0	2	0	0	2
<i>Lutjanus analis</i>	0	0	2	0	0	2
<i>Bothus lunatus</i>	0	0	1	1	0	2
<i>Cosmocampus elucens</i>	0	0	1	1	0	2
<i>Bodiamus rufus</i>	1	1	0	0	0	2
<i>Mulloidichthys martinicus</i>	2	0	0	0	0	2
<i>Pomacanthus paru</i>	2	0	0	0	0	2
<i>Scomberomorus regalis</i>	0	0	1	0	0	1
<i>Sphyraena picudilla</i>	0	0	1	0	0	1
<i>Diodon hystrix</i>	1	0	0	0	0	1
<i>Doratonotus megalepsis</i>	1	0	0	0	0	1
<i>Cephalopholis cruentata</i>	1	0	0	0	0	1
<i>Gerres cinereus</i>	1	0	0	0	0	1
<i>Gobiosoma</i> spp.	1	0	0	0	0	1
<i>Hypoplectrus gummigutta</i>	1	0	0	0	0	1
<i>Hypoplectrus nigricans</i>	1	0	0	0	0	1
<i>Lactophrys</i> spp.	1	0	0	0	0	1
<i>Scorpaena</i> spp.	0	1	0	0	0	1
<i>Synodus foetens</i>	0	1	0	0	0	1

sons (ANOVA, $P = 0.113$, $df = 3$, 20; Figure 3). Post hoc tests showed that species richness in patch reefs and rubble was significantly higher than seagrass, algal beds, and sandy bottom types (Tukey's test, $P < 0.001$). There was no significant interaction between habitat type and season in species richness (ANOVA, $P = 0.082$, $df = 12$, 20; Figure 3).

Variation in fish density

Fish density was significantly different among habitat types (ANOVA, $P < 0.001$, $df = 4$, 20) and seasons (ANOVA, $P < 0.002$, $df = 3$, 20), but there was no interaction between the main effects (ANOVA, $P < 0.360$, $df = 12$, 20; Figure 4). Fish density was significantly highest in patch reefs and rubble relative to seagrass, algal beds and sandy habitat types across all seasons (Tukey's test, $P < 0.001$). Comparisons of fish density pooled by habitat type indicated that fish density observed in summer was statistically higher than in the spring and winter season (Tukey's test, $P < 0.05$).

Similarity of fish faunas among habitat type and season

Fish assemblages recorded from each habitat type tended to cluster together (Figure 5) showing a comparatively high degree of similarity; season appeared to have no effect. Fish assemblages observed over patch reefs and rubble were more similar to each other than to those observed in vegetated and unvegetated habitat types. Unvegetated habitat types clustered together separately from all other habitat types.

Variation in density of economically important species common species by habitat type

Acanthurus chirurgus recruits (< 5 cm) and sub-adults /m² (5–10 cm, > 10 cm) were higher in patch reefs and rubble (Figure 6a) than any other habitat types (ANOVA, $P < 0.001$; $df = 4$, 8; Tukey's test, $P < 0.001$). Density of newly settled grunts/m² (*Haemulon* spp., < 3 cm) were higher on algal plains compared with other habitat types (ANOVA, $P < 0.001$; $df = 4$, 8; Tukey's test, $P < 0.009$;

Figure 3. Plot of the mean (s) species richness by habitat type observed during different seasons. s = standard deviation.

Figure 6b). *Scarus iseri* recruits/m² (< 5 cm) were more dominant in patch reefs (Figure 6c), than juveniles (5–10 cm) and sub-adults (> 10 cm)/m² (ANOVA, $P < 0.01$; $df = 4, 8$; Tukey's test, $P < 0.001$). *Ocyurus chrysurus* recruits (< 5 cm)/m² were highest on algal plains and seagrass while larger individuals (> 10 cm) were most abundant on patch reefs (ANOVA, $P < 0.01$; $df = 4, 8$; Tukey's test, $P < 0.02$; Figure 6d). Density (ind/m²) of size class > 5 cm was almost exclusively found in patch reefs for *Haemulon plumieri* (ANOVA, $P < 0.001$, $df = 4, 8$; Tukey's test, $P < 0.003$; Figure 6e) and *H. flavolineatum* (ANOVA, $P < 0.001$, $df = 4, 8$; Tukey's test, $P < 0.002$; Figure 6f). There were no significant interaction terms among habitat type and size class for fish density for all species studied (ANOVA, $P < 0.05$, $df = 8, 20$).

Figure 5. Cluster analysis of fish density by habitat type and season based on visual census using the Bray-Curtis similarity metric and average linkage clustering techniques.

Figure 4. Plot of the mean (s) fish density by habitat type observed during different seasons. s = standard deviation.

Occurrence and density of recruits and non-recruits of common fish species

Recruit density of *H. bivittatus* (ind/m²) was highest in patch reef habitat in summer relative to other habitat types (ANOVA, $df = 4, 20$, $P < 0.001$; Tukey's test, $P < 0.001$; Figure 7a). *Haemulon bivittatus* sub-adults (5–10 cm, > 10 cm) showed significant seasonal differences in density (ind/m²) (ANOVA, $P < 0.004$, $df = 3, 20$; Figure 7b), with the highest mean density being recorded in winter over patch reefs for both size classes (Tukey's test, $df = 4$, $P < 0.001$; Figure 7c). There were no significant interaction terms between habitat type and season for *H. bivittatus* recruits (ANOVA, $P = < 0.686$, $df = 12, 20$) and *H. bivittatus* sub-adults (ANOVA, $P < 0.902$, $df = 12, 20$). A higher density (ind/m²) of newly settled grunts (*Haemulon* spp.) was observed over algal beds during summer and fall seasons (ANOVA, $P < 0.01$; $df = 4, 20$; Tukey's test, $P < 0.009$; Figure 7d). No significant interaction terms between habitat type and season were found for newly settled grunts *Haemulon* spp. density (ANOVA, $P < 0.578$, $df = 12, 20$).

Non-recruit grunt (*Haemulon* spp) density (ind/m²) (5–10 cm) was significantly highest in spring (ANOVA, $P < 0.004$, $df = 4, 20$; Tukey's test, $P < 0.01$; Figure 7e) over patch reef habitats, whereas the density (ind/m²) of grunt >10 cm in patch reefs were highest during summer (Figure 7f). There were no significant interaction terms between habitat type and season in non-recruit *Haemulon* spp. density (ANOVA, $P < 0.563$, $df = 12, 20$).

DISCUSSION

Differences in species richness and fish density

The nearshore environment within St. Croix's south-east bank barrier reef lagoon exhibited distinct patterns in the distribution of fish assemblages among seagrass, algal plains, patch reefs, rubble, and sandy habitat types. The

Figure 6. Plot of density of economically important species by size class and habitat types: 6a) *A. chirurgus*, 6b) *O. chrysurus*, 6c) *Haemulon* spp., 6d) *S. iserti*, 6e) *H. flavolineatum*, 6f) *H. plumierii*.

seagrass and algal plain were dominated by small resident species, such as *Halichoeres* spp. and *S. radians*, and by juveniles of non-resident species like *Haemulon* spp. and *O. chrysurus*. Rubble and patch reefs harbored higher species richness and were mostly dominated by small juvenile damselfishes, parrotfishes, grunts, and doctorfishes. The highest species richness occurred over patch reefs and rubble, than over vegetated habitat type types (seagrass, algal plains) and unvegetated sandy habitat types during all 4 seasons. Fish densities were also higher in patch reefs and rubble than over seagrass, algal plains, and sandy bottoms.

Fish assemblages in physically 'structured environments' (patch reef and rubble) tend to be more similar to each other than to those in vegetated (seagrass/algal beds) and unvegetated habitat types (sand) (Nagelkerken et al. 2000, Adams and Ebersole 2002). The cluster analysis

based on our data confirms this pattern, illustrating that fish assemblages from patch reef, and rubble habitat types were more similar to each other, but different from assemblages associated with seagrass, algal plain, and sandy habitat types, regardless of season. Nagelkerken et al. (2000) and Adams and Ebersole (2002) similarly observed a hierarchy in fish abundance within highly structured habitat types (patch reefs, rubble, cobbler) possessing higher density followed by seagrass and then algal beds, and over unvegetated sand bottom.

Seasonal Distribution

Seasonal changes in species composition and density of fish populations were major characteristics in our near-shore lagoonal habitat types. Peak density of total fishes occurred during summer, with a secondary peak in fall and the lowest density of total fishes in winter. Although

Figure 7. Plot of seasonal occurrence of common species by habitat type: 7a–c) *H. bivittatus*; 7d–f) *Haemulon* spp.; < 5 cm, 5–10 cm, > 10 cm, respectively.

recruits were mainly abundant in the latter half of the summer and in the fall, the pattern of habitat type use by settlers and juveniles differed by species and season. For example, 50% of all recruits occurred in late summer whereas 42% occurred in Fall and 8% in the rest of the year. Tropical fish assemblages have shown seasonal fluctuation characterized both by a higher species richness and by a higher abundance of fishes during the summer and fall, which is influenced by recruitment of juveniles, the increase of food availability, and spawning patterns (Ogden and Gladfelter 1983, Baelde 1990). Considering that much of the research of settling and juvenile fishes in the Caribbean has taken place during the summer, future research should focus on the relative mechanism of transport processes throughout the year.

Habitat type distribution

Distinct patterns of species among habitat types were observed at St. Croix's southeastern barrier reef lagoon

with some species being found exclusively or predominantly in one of the 5 habitat types. The scarid, *C. roseus*, and the labrid, *H. poeii*, for example, were more associated with seagrass, whereas other labrids such as *T. bifasciatum* and *H. radians*, the scarids *S. aurofrenatum*, *S. iseri*, and *S. viride*, and the squirrelfishes *H. adensionis* and *M. jacobus* were found predominantly over patch reefs. Fish species found predominantly over bare sand were *X. martinicensis* and *C. glaucocraenum*. In contrast, *H. bivittatus*, *S. radians*, newly settled grunts *Haemulon* spp., *H. flavolineatum*, *H. plumieri*, the lutjanids *O. chrysurus* and *L. mahogoni*, and the acanthurids *A. chirurgus* and *A. bahianus* were commonly associated with more than one habitat type. The differences in fish size distributions among habitat types suggested different ontogenic distribution patterns by species. For example, many recruits of economically important species (e.g., *S. iseri*, *A. chirurgus*) were on patch reefs and rubble whereas recruits of newly settled *Haemulon* spp. and *O. chrysurus* were mostly in

seagrass beds and algal plains. Density of larger (> 10 cm) fish (e.g., *H. plumierii*, *S. iseri*, *H. flavolineatum*, and *O. chrysurus*) were low in patch reefs and seagrass beds, however. These results reflect the temporary and successive use of seagrass and patch reef habitats by juveniles of various species that move elsewhere as they grow, as it is the case for *O. chrysurus*, and *S. iseri* (Clifton 1991, Tolimieri 1998, Nagelkerken et al. 2000, Cocheret de la Morinière et al. 2002). Changes in habitat type use might also be expected to coincide with size-related changes in individual fitness or physiological requirements (Appeldoorn et al. 1997, Lindeman et al. 1998), or ontogenetic changes in diet, mortality, and/or competitive interactions (Shulman and Ogden 1987, Nagelkerken et al. 2000, Cocheret de la Morinière et al. 2002). For example, some snappers, grunts, and parrotfishes progressively change habitat type with size (Appeldoorn et al. 1997, Lindeman et al. 1998, Adams and Ebersole 2002). *Ocyurus chrysurus*, *H. flavolineatum*, and *H. plumierii* settle onto seagrass beds and algal plains and migrate to nearby reefs at larger sizes (Shulman and Ogden 1987, Appeldoorn et al. 1997, Lindeman et al. 1998). Distribution of *S. iseri* appears to be determined by habitat-based distribution of primary food sources (Clifton 1991, Tolimieri 1998). As their foraging efficiency and home range increases ontogenetically, these nursery areas no longer provide adequate shelter and food sources; thus, the species migrate to deeper habitat like fore-reef and mid-shelf reef to meet their ecological requirements (Clifton 1991, Tolimieri 1998).

Our study suggests that nursery habitats are not limited to seagrass and mangrove systems, but include other nearshore habitats like patch reefs, rubble areas, and algal plains. Patch reefs and rubble habitats had the highest density of fish recruits; however, total counts of fish recruits were higher on seagrass beds and algal plains because of the areal coverage of these latter habitat types in the bays surveyed (Figure 2). In the Caribbean, recent studies of nearshore fish assemblages suggest that patch reefs and rubble areas appear to be important shelter sites for juvenile fishes in mangrove and seagrass dominated lagoons (Risk 1997, Nagelkerken et al. 2000, Adams and Ebersole 2002). For example in Curaçao, shallow-water coral reefs were utilized more by *H. chrysargyreum*, *L. mahogoni*, *A. bahianus*, and *A. saxatilis* as nursery areas than seagrass and mangrove lagoons (Nagelkerken et al. 2000). In southwestern Puerto Rico, *H. flavolineatum*, *O. chrysurus*, and *H. plumierii* showed greater preference for shallow coral reefs as nursery areas than mangrove and seagrass (Murphy 2001). Finally, similar patterns of habitat use were noted for *H. flavolineatum*, *A. bahianus*, and *A. chirurgus* as they were not strictly dependant on

mangroves and seagrass as nurseries but used alternative nursery areas like shallow coral reefs and rubble areas in St Croix (Risk 1997, Adams and Ebersole 2002).

However, to evaluate the role of nearshore habitat types as fish nursery, more studies should be done focusing in understanding how these habitat types may provide a nursery function role to reef fishes. During a study of seagrass and mangrove fishes in Belize, Chittaro et al. (2005) found that based on density, assemblage composition, and relative rates of predation, not all mangrove and seagrass beds appeared to offer nursery function. Their study highlighted the need to avoid generalizations about mangroves and seagrass having nursery related functions, if estimates of density are the only method to confirm nursery potential. Additionally, in the Indo-Pacific, the nursery value of mangroves and seagrass have been questioned as juvenile fishes did not show evidence of using mangroves as shelter (Thollot, 1992, Huxham et al. 2004). Therefore, many factors like density, survival, growth, and movement among habitat types have to be examined simultaneously in order to support a particular habitat type as being a nursery (Beck et al. 2001).

Implications for management

Knowledge of habitat type use patterns by different fish life stages along a cross-shelf gradient is needed to understand the importance of nearshore habitats as nursery areas and presumable ontogenetic shifts in habitat type requirements. Based on these data, it would then be possible to infer connectivity of reef fish migrating among habitat types from inshore to offshore during post-settlement ontogeny (Appeldoorn et al. 1997, Lindeman et al. 1998, Nagelkerken et al. 2000). Determination of nursery value of nearshore habitats and ontogenetic shifts in fish habitat type use (Appeldoorn et al. 1997, Lindeman et al. 1998, Cocheret de la Morinière et al. 2002) would facilitate fisheries conservation and coastal zone management plans. For example, designing marine protected areas (MPAs) and improving the efficacy of the proposed MPAs in areas adjacent to the St Croix East End Marine Park.

As our study suggests, there is increasing evidence that many reef fish are dependent on nearshore systems that comprise a mosaic of habitat types including not only coral habitat structure but also a mixture of seagrass, algal plains, and rubble. Each of these habitat types contains unique biotic communities that vary differently depending on the scale at which individual or community level processes are observed. Strong linkages exist between fish and habitat and successful implementation of marine reserves requires knowledge of location, distribution, and extent of habitat types necessary for successful recruit-

ment, growth, feeding, and reproduction. To measure the efficacy of a marine reserve to enhance fish abundance, it is critical to develop a baseline against which future estimates can be compared. The results found in this study provide a foundation upon which an ecosystem approach could be developed. As resource managers address the placement and design of MPA's, information on habitat type use and life-history characteristics of coral reef fishes are required and will become a vital part of the decision-making process. The use of lagoon habitat types as nurseries by reef-associated fishes must be incorporated into any management plan.

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