

Functional Feeding Groups, Species Richness and Spatial Distributions of Fishes in Rocky and Sandy Beach Habitats of St. John, U.S. Virgin Islands

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ABSTRACT

Objectives were to identify and compare fish species richness, functional feeding group richness and diversity, and delineate distributions of fishes at rocky and sandy beach habitats at St. John, U.S. Virgin Islands. Visual observations using snorkel and mask were made at 3-m intervals seaward from shore during daylight hours. A total of 69 taxa (67 species) representing 33 families of fishes were observed. Total (53) and average fish species richness (32.7) at rocky beach habitats were greater than those (total=43; average=24.3) at sandy beach habitats. Twelve functional feeding groups were identified (diurnal planktivores, excavators/eroders, macroalgae browsers, macrocarnivores, mobile benthic invertivores, general omnivores, strict piscivores, sand invertivores, scrapers, coral/colonial sessile insectivores, territorial algae/detritus, and turf grazers). Total numbers of functional feeding groups (range=10-12) and species (range=29-46) per functional feeding groups at distances greater than 1 m from shore at rocky beach habitats were consistently higher than those (functional feeding group range=8-10; species per functional feeding group=19-30) at sandy beach habitats. Information on the number and composition of functional feeding groups in rocky and sandy beach habitats from this study can serve as a baseline for future investigations as changes in Caribbean habitats continue to occur.

Keywords: fish species richness, fish functional feeding group, Caribbean beach habitats

INTRODUCTION

Substrate complexity such as that offered by coral reefs is significant in providing diverse habitats that harbor a variety of fishes, particularly reef fishes (Christensen et al., 2003; Claro et al., 2001; Friedlander and Parrish, 1998; Gratwicke and Speight,

2005; Mac et al., 1998; Monaco et al., 2003; 2007; Nero and Sealey, 2005; Ohman and Rajasuriya, 1998). Other habitat areas, such as Caribbean mangroves and seagrass beds, are also important habitats as they serve as nursery and feeding areas for a variety of juvenile reef fishes (Faunce and Serafy, 2006; Nagelkerken and van der Velde, 2002). Focus on the decline of coral reefs and mangroves and the various ecological functions they provide to reef fishes has overshadowed habitats (i.e., sandy and rocky nearshore habitats) considered to be lesser important in understanding the health and dynamics of tropical ecosystems and their ichthyofaunas (Nero and Sealey, 2005). Granted, fish communities in sandy and rocky beaches have relatively depauperate ichthyofaunas compared to those of reef systems. Sandy and rocky nearshore habitats, however, harbor some of the same fish species common to reefs, mangroves, and seagrass beds (Valdez-Munoz and Mochek, 2001; Ortiz and Lalana, 2008). Except for some observational data on selected species in nearshore sandy and rocky Caribbean habitats provided by Valdez-Munoz and Mochek (2001), there is a paucity of published information on the fishes in sandy and rocky beach habitats in the Caribbean. Knowledge of species richness and distributions of fishes in nearshore sandy and rocky-shore habitats can also serve as baseline data for future comparisons as changes occur in reef, mangroves, and seagrass habitats related to chronic anthropogenic impacts (e.g. overfishing, habitat degradation) and climate change. For example, upwards of 90 % of reefs of the U.S. Virgin Islands (USVI) experienced bleaching in 2005 when sea surface temperatures were higher than the previous 14 years (Rothenberger et al., 2008). Of particular importance may be the number and composition of functional feeding groups in these habitats, where the loss of one or two functional feeding groups represented by one or few species could be critical to the functioning of the ecosystem (Halpern and Floeter, 2008).

Objectives of this study were to identify and compare fish species richness, functional feeding group richness and diversity, and delineate distributions of fishes at sand- and rock-shoreline beach habitats at St. John, U.S. Virgin Islands in the Caribbean Sea.

MATERIALS AND METHODS

Fish species richness and spatial distributions were surveyed by visual census using snorkel and mask at each of 1, 3, 6, 9, 12, 15, and 20 m from shore at each of 30 transects (14 sandy- and 16 rocky-shoreline habitats) at Little Lameshur (18.32026 N, -64.72551 W), Great Lameshur (18.31822 N, -64.72427 W), and Francis Beach (18.36537 N, -64.74365 W), St. John, USVI, during daylight hours (i.e., 0800-1800) from 12-18 July 2007 and 8-18 July 2008. Transects were established randomly at each rocky or sandy beach habitat, and none were re-sampled during the second year. Low light conditions and poor visual acuity at greater depths precluded the recording of species beyond 30 m from shore. The vertical observational zone was from the bottom substrate to the surface, including boulder ledges and crevices. No substrate material was overturned or dislodged. Fishes within an estimated 3-m horizontal circumference of the observer were identified by visual observation. Some identifications were verified by examining digital photographs made underwater with an Olympus Stylus 770 SW or Olympus 850 SW camera at each distance per transect. Water depth (m) was measured with a weighted cord marked in 1-m increments. Relative percents of habitat composition (i.e., sand, gravel, cobble, boulder, seagrass,

and coral) were estimated by observation and recorded at each distance from shore. These percents were transformed to their arcsin equivalents prior to statistical analysis. Fish census data are available upon request.

Assignment of species to functional feeding groups (diurnal planktivores, excavators/eroders, macroalgae browsers, macrocarnivores, mobile benthic invertivores, general omnivores, strict piscivores, sand invertivores, scrapers, coral/colonial sessile insectivores, territorial algae/detritus, and turf grazing) follows the designations in Halpern and Floeter (2008). Species richness, and functional feeding group richness, Shannon-Weiner diversity and evenness were compared among (general linear model followed by Duncan's Multiple Range Test at $p=0.05$, SAS, 2009) and between (t-test at $p=0.05$, SAS, 2009) rocky and sandy shore habitats.

RESULTS

Average water depths (1.6-4.6 m) at each distance from shore (3, 6, 9, 12, 15, and 20 m) at rocky transects were significantly greater than those (0.94-2.5 m) at sandy transects (Table 1). Percent occurrences of coral, boulder and seagrasses at rocky habitats were significantly higher than those from 3-20 m from shore at sandy habitats with three exceptions (Table 1). Percent occurrence of coral at 15 and 20 m and that of seagrasses at 20 m from shore did not vary significantly between rocky and sandy habitats (Table 1). Conversely, percent occurrences of cobble, gravel, and sand at rocky habitats were significantly lower than those at sandy habitats from 3-20 m from shore with two exceptions. Occurrence of sand and gravel at 20 m from shore did not vary significantly between rocky and sandy habitats (Table 1).

A total of 69 taxa (67 species + 2 families) representing 33 families of fishes were observed (Table 2) in the 30 sandy and rocky transects at Little Lameshur, Francis Beach, and Great Lameshur, St. John, USVI. The most speciose families were Scaridae (8), Haemulidae (7), Pomacentridae (6), Labridae (4), and Lutjanidae (4). Seventeen families were each represented by one species. Total fish species richness at rocky habitats was 53; that at sandy habitats was 43. Average number of species (32.7) at rocky habitats was significantly greater than that (24.3) at sandy habitats ($t=6.18$; $p=0.0016$). Species richness (avg. range=11-20) at combined rocky habitats did not vary significantly at distances 6-20 m from shore (Table 3). In contrast, at combined sandy habitats, species richness (avg. range=1-5.9) did not vary significantly at distances 1-20 m from shore (Table 4). Species richness (avg. range 3-20) at each distance from shore at rocky habitats was significantly greater than those (avg. range=1-5.9) at sandy habitats (Table 5).

Numbers of functional feeding groups encountered at rocky habitats were consistently higher than those at sandy habitats (Tables 6-7). On average, rocky habitats from 3-20 m from shore had two more functional feeding groups (avg.=11.3) than sandy habitats (avg.=9.3; Tables 6-7). Two species (*Archosargus rhomboidalis* and *Sparisoma radians*) of the macroalgae browser functional feeding group occurred frequently at rocky habitats. No macroalgae browsers were observed at sandy habitats. The most speciose functional feeding groups were mobile benthic invertivores (11 species at 9 m in rocky habitats), scrapers and piscivores (each 9 species at 6 m in rocky habitats), and macrocarnivores (6 species at 6 m in sandy habitats)(Table 2). Total numbers of functional feeding groups (range=10-12) and species (range=29-46) per functional feeding groups at distances greater than 1 m from shore at rocky habitats

were consistently higher than those (functional feeding group range=8-10; species per functional feeding group=19-30) at sandy habitats (Tables 1, 6-7). At the 1-m distance, functional feeding group richness at rocky habitats was five; that of the 1-m sandy habitat was one.

Except at 20 m from shore, functional feeding group richness (avg. range=6.67-10) and Shannon diversity (avg. range=1.84-2.05) from 3-15 m from shore at rocky habitats were significantly higher than functional feeding group richness (avg. range=5.33-8.33) and Shannon diversity (avg. range=1.43-2.02) at sandy habitats (Table 8). In contrast, functional feeding group richness (avg.=7.3) and diversity (avg.=1.86) at 20 m from shore at sandy habitats were significantly greater than functional feeding group richness (avg.=6.67) and diversity (avg.=1.53) 20 m from shore at rocky habitats (Table 8). Functional feeding group evenness indices (avg. range=0.8896-0.9171) at distances 6-20 m from shore at rocky habitats were significantly lower than those (avg. range=0.9226-0.9551) at sandy habitats (Table 8), indicating greater variability in numbers of species comprising the functional feeding groups in rocky habitats. For example, at 6 m from shore at rocky habitats, mobile benthic invertivores and scrapers totaled 10 and 9, respectively, whereas other functional feeding groups were composed of 1-5 species. At 3 m from shore, the average functional feeding group evenness index (0.9764) at rocky habitats was significantly greater than that (0.9539) at sandy habitats (Table 8).

DISCUSSION

Comparison of rocky and sandy beach habitats

The more complex habitats of the intermingled boulder, rock, and coral substrates at rocky habitats exhibited higher species richness and functional feeding group richness than did less complex sandy habitats. Rocky shore habitats, where fish species richness was correlated with increasing water depth and the presence of coral, boulders, cobble, and gravel, harbored more fish species (avg.=32.7) than did sandy habitats (avg.=24.3). Even at greater distances from shore (i.e., 15 and 20 m) at sandy habitats where the percentages of coral (6.0-6.2) and seagrass (26.0 at 20 m) were comparable to those (coral=5.5-7.4; seagrass=23.5 at 20 m) at the same depths at rocky beaches, species richness (avg. range=3.73-5.89) still was significantly lower than those (avg. range=11.0-12.8) at rocky habitats. That more complex habitats support greater fish species richness has been documented repeatedly in the literature (Christensen et al., 2003; Claro et al., 2001; Friedlander and Parrish, 1998; Gratwicke and Speight, 2005; Monaco et al., 2003; 2007; Nero and Sealey, 2005; Ohman and Rajasuriya, 1998; Valdez-Munoz and Mochek, 2001). Results from the present study are comparable to those of Gratwicke and Speight (2005) who studied the relationship between fish species richness and habitat complexity in a series of shallow tropical marine habitats in the British Virgin Islands. The lower species richness (range = 1-30) at sandy beach habitats is comparable to the findings of Valdes-Munoz and Mochek (2001) who reported low fish species diversity in non-estuarine sandy beach areas of Cuba where species richness was 25. Although vertical relief of substrates (e.g. boulder rock substrates) was not measured in the present study, average depth, distance from shore and percentage of rock were correlated with high species richness at rocky habitats. These results are not unlike those of Brokovich et al. (2006), who indicated that reef fish assemblages in the northern tip of the Red Sea varied between habitats, and that

fish community structure was best explained by average depth, distance from shore, vertical relief, percent cover by rock, and cover complexity index.

Species richness and both the number and composition of functional feeding groups in rocky and sandy habitats may have applications in future studies as changes in Caribbean habitats continue to occur. For example, Halpern and Floeter (2008) point out that knowledge of the functional feeding groups provide insight into the assembly, structure and dynamics of ecological communities, and that the addition or loss of a few species can have significant to minimal impacts on ecosystem function. On average, rocky habitats from 3-20 m from shore had two more functional feeding groups (avg.=11.3) than did sand habitats (avg.=9.3). However, the numbers of species comprising the functional feeding groups at rocky habitats averaged 13.3 species (range 5-46) more than those at sandy habitats (range 1-30). In both rocky and sandy habitats, many functional feeding groups (i.e., turf grazer, excavator eroder, macroalgae browser, and territorial algae detritivore) were represented by only one or two species, with most single species functional feeding groups occurring in sandy habitats (Table 2).

Spatial and behavioral comparisons of fishes

Spatial and behavioral descriptions, and occurrences of diurnal inshore pelagic fishes, epibenthic pomacentrids, suprabenthic resident reef fishes, and territorial benthic fishes of the Cuban shelf provided by Valdes-Munoz and Mocheke (2001) present the single most detailed source for comparisons with fishes in rocky and sandy beach habitats in our study.

Diurnal inshore pelagic fishes

Valdes-Munoz and Mocheke (2001) reported the diurnal, transient belonid, carangid, and sphyraenid species common in the inshore upper water column at study sites in Cuba. We encountered these same transient taxa at our inshore rocky and sandy habitats, but also observed atherinid, engraulid, and clupeid (e.g. *Harengula humerali*) schools in the upper water column at these habitats as well.

Diurnal Epibenthic pomacentrids

The epibenthic pomacentrid, *Abudefduf saxatilis* (sergeant major) was reported by Valdes-Munoz and Mocheke (2001) to be common on irregular bottom types and frequently formed large schools 95 % of the time they were observed. In contrast, we encountered individual *A. saxatilis* and never observed schools of *A. saxatilis* over nearshore rocky or sandy substrates. Valdes-Munoz and Mocheke (2001) observed the epibenthic pomacentrid (blue chromis), *Chromis cyanea* (abundant in the Caribbean), forming large schools. We never observed a single *C. cyanea* at any of our rocky or sandy habitats, suggesting that these habitat substrates are not favorable to this species.

Diurnal suprabenthic fishes

Suprabenthic fishes (i.e., scarids, acanthurids, labrids, and chaetodontids), diurnally foraging above the bottom, were the resident fishes living over reefs serving as the primary representatives of the reef fish community studied by Valdes-Munoz and Mocheke (2001). They reported scarids occurring in small groups or alone, constantly moving over great distances during the day while foraging on coral; in sea grass beds; however, some scarid species (e.g. *Sparisoma radians*) showed some behavioral elements of nomadic fishes, a high degree of motor activity, and the formation of large schools. We never observed large schools of any of the scarids (i.e., *Scarus iserti*, *Scarus taeniopteryx*, *Sparisoma viride*, *Sparisoma aurofrenatum*, *Sparisoma*

frondosum, *Sparisoma radians*, and *Sparisoma rubripinne*) in our study. We observed these species foraging on coral singly or within close proximity of other scarids. Three scarid species (*S. aurofrenatum*, *S. frondosum*, and *S. radians*) occurred at rocky habitats but were never observed at sandy habitats in our study.

Our observations of the acanthurids (*Acanthurus bahianus*, *Acanthurus chirurgus*, and *Acanthurus coeruleus*), spending most of their time on the bottom while grazing during the day, are consistent with the behaviors of the species reported by Valdes-Munoz and Mochek (2001). Whereas we observed some intraspecific aggression between individuals in these species, we never observed the formation of schools reported by Valdes-Munoz and Mochek (2001) probably because of the low density of individuals in the rocky and sandy habitats we studied.

Labrids, reported by Valdes-Munoz and Mochek (2001) to be one of the most common families foraging during the daytime, were common in both rock and sand beach habitats in our investigation. Five labrid species, *Halichoeres bivittatus*, *Halichoeres maculipinnia*, *Halichoeres radiatus* (juveniles only), *Lachnolaimus maximus*, and *Thalassoma bifaciatum*, were constantly on the move in search of food. In particular, our observations of *H. bivittatus* and *T. bifaciatum* are consistent with the movements and behaviors described by them, where the latter species was reported to be in a fast and constant motion for 99 % of their time while foraging over reefs on the Cuban shelf. We cannot, however, confirm their observations of group formation in *T. bifaciatum*.

Our observations of diurnal feeding behaviors near the bottom by *Chaetodon striatus*, *Chaetodon capistratus*, and *Chaetodon ocellatus* are consistent with those described by Valdes-Munoz and Mochek (2001). We did not observe any of these chaetodontids protecting territories, consistent with the report by Valdes-Munoz and Mochek (2001).

Diurnal territorial benthic fishes

Juvenile to adult *Stegastes leucostictus* (beaugregory) were observed to protect their territories against conspecific individuals during the daytime. These observations are consistent with descriptions of aggression of this territorial benthic species reported by Valdes-Munoz and Mochek (2001). *Stegastes diencaeus* (longfin damselfish) were commonly observed defending the confines of basket sponges in both rocky and sandy beach habitats.

Diurnal observations of nocturnal suprabenthic fishes

This group of primarily nocturnal species is composed of lutjanids, haemulids, and holocentrids. Valdes-Munoz and Mochek (2001) indicated that grunt and snapper aggregations are the largest among the species associated with the bottom, and are most active at night when they move off reefs and forage in neighboring areas. In our daytime study, small to large (>300 individuals) motionless or slow moving schools of juvenile to adult *Haemulon flavolineatum* (French grunt) and juvenile *Haemulon sciurus* (bluestripe grunt) occurred at both rocky and sandy beach habitats, usually in areas of cover such as overhanging boulders, submerged trunks of fallen trees or rock ledges. Adult *H. sciurus*, *Haemulon melanurum* (cottonwick) and *Haemulon parra* (sailor's choice) were observed usually as single individuals, not in schools. Only once did we observe two adult *H. parra* under a boulder. Juvenile *Lutjanus synagris* (lane snapper) and juvenile *Ocyurus chrysurus* (yellowtail snapper) were observed in schools hovering over the bottom. Adult *L. synagris* and *O. chrysurus*, as well as adult

Lutjanus analis (mutton snapper) and *Lutjanus apodus* (schoolmaster) were observed individually, not in schools. These observations of juvenile and adult grunts and snappers in our study areas are consistent with the findings of Valdes-Munoz and Mochek (2001) who reported the activities of these species in Cuban reef systems.

The nocturnal holocentrids, *Holocentrus rufus* (longspine squirrelfish) and *Myripristis jacobus* (blackbar soldierfish) were common to both rocky and sandy habitats. They were seen underneath overhanging rock ledges or under boulders where they remained motionless. They were frequently accompanied in these protected areas by juvenile and adult *H. flavolineatum* and *H. sciurus*.

Notes on other species at beach habitats

Individual *Synodus saurus* (bluestripe lizardfish) frequented sandy nearshore areas where they buried themselves tail first into the sand. Remaining motionless with only their eyes exposed, they ambushed small fishes that were within striking range, which was about equal to their total body length. Also common in sandy substrates were two bothids, *Bothus lunatus* and *Bothus ocellatus*. These flatfishes buried themselves in the sand at nearshore sandy habitats too, where they laid motionless with only their eyes exposed above the sand to ambush passing fishes. Individual or groups of up to three *Pseudopeneus maculatus* (spotted goatfish) were common foragers in sand areas of both habitats studied. Two carangids, *Caranx ruber* (bar jack) and *Trachinotus goodei* (palometa) were also common pelagic species at both beach habitats.

Although the blenniid (*Scartella cristata*) and the gobiid (*Bathygobius soporator*) were recorded from both rocky and sandy habitats less than three times each, their occurrences were probably underrepresented because of their cryptic behaviors and small sizes. Similarly, low frequencies of blenniid and gobiid species were also reported by Lindeman and Snyder (1999) in a study of nearshore hard bottom fishes of southern Florida.

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TABLE 1. Comparison of water depth (m), and percent cover of substrate type between rocky and sandy beach habitats at combined Little Lameshur, Francis and Great Lameshur beaches, St. John, USVI in July 2007 and July 2008.

Parameter	Distance from shore (m)	Rocky	Sandy	F	p > F
	1				
Depth		0.20	0.17	0.14	0.7247
Coral		0.0	0.0	-	-
Boulder		81.7	0.0	2.21	0.007
Cobble		3.3	0.0	1.0	0.3739
Gravel		0.0	10.0	3.0	0.1583
Sand		15.0	90.0	135.0	0.0003
Seagrass		0.0	0.0	-	-
	3				
Depth		1.56	0.94	6.40	<0.0001
Coral		1.10	0.00	3.91	0.0514
Boulder		49.60	0.00	392.47	<0.0001
Cobble		10.60	32.20	21.99	<0.0001
Gravel		4.40	30.00	19.58	<0.0001
Sand		17.80	33.80	8.00	0.0059
Seagrass		12.60	0.00	60.32	<0.0001
	6				
Depth		1.91	1.10	23.97	<0.0001
Coral		3.42	0.00	34.00	<0.0001
Boulder		48.30	0.00	3105.74	<0.0001
Cobble		11.40	40.70	69.47	<0.0001
Gravel		4.02	10.68	8.29	0.0045
Sand		13.84	43.18	76.09	<0.0001
Seagrass		12.68	5.15	17.88	<0.0001
	9				
Depth		2.84	1.22	103.28	<0.0001
Coral		2.92	0.00	33.21	<0.0001
Boulder		43.00	1.50	4957.44	<0.0001
Cobble		5.17	22.29	40.24	<0.0001
Gravel		2.50	6.88	28.39	<0.0001

TABLE 1 continued

Parameter	Distance from shore (m)	Rocky	Sandy	F	p > F
Sand		17.17	64.00	282.35	<0.0001
Seagrass		24.58	5.57	64.46	<0.0001
	12				
Depth		2.76	1.29	89.87	<0.0001
Coral		7.46	0.00	104.02	<0.0001
Boulder		48.31	0.00	5870.34	<0.0001
Cobble		6.76	34.17	33.87	<0.0001
Gravel		3.38	5.42	3.99	0.0484
Sand		12.54	58.47	115.23	<0.0001
Seagrass		7.18	0.97	10.32	0.0017
	15				
Depth		4.10	2.00	175.68	<0.0001
Coral		5.47	6.23	0.20	0.6532
Boulder		38.52	6.23	362.87	<0.0001
Cobble		4.06	31.98	44.00	<0.0001
Gravel		1.02	3.02	18.43	<0.0001
Sand		22.42	40.28	14.23	0.0003
Seagrass		33.52	12.26	34.64	<0.0001
	20				
Depth		4.61	2.49	180.83	<0.0001
Coral		7.39	6.00	0.53	0.4681
Boulder		34.89	7.00	122.92	<0.0001
Cobble		4.32	36.33	33.31	<0.0001
Gravel		0.00	0.56	3.71	0.0574
Sand		18.07	24.11	1.85	0.1771
Seagrass		23.52	26.00	0.20	0.6576

TABLE 2. Comparisons of functional feeding groups (FFG) and taxa per group by distance from shore (m) between rocky and sandy beach habitats at St. John USVI, July 2007 and July 2008. Functional feeding group designations from Halpern and Floeter (2008).

Distance from shore (m)	Functional Feeding Group	FFG Richness		Taxa	Occurrence	
		Rocky beach habitats	Sandy beach habitats		Rocky beach habitats	Sandy beach habitats
1	Diurnal planktivore	2	1	Atherinidae	X	
				Engraulidae	X	X
	Macrocarnivore	1		<i>Gerres cinereus</i>	X	
	Piscivore	1		<i>Eucinostomus jonesi</i>	X	
	Territorial algae detritivore	1		<i>Stegastes leucostictus</i>	X	
	Group Total	5	1			
3	Diurnal planktivore	3	2	Atherinidae	X	
				Engraulidae	X	X
				<i>Thallasoma bifasciatum</i>	X	
				<i>Opistognathis macrognathus</i>		X
	Macrocarnivore	5	5	<i>Dasyatus americana</i>		X
				<i>Gerres cinereus</i>	X	X
				<i>Lutjanus apodus</i>	X	
				<i>Lutjanus synagris</i>	X	X
				<i>Ocyurus chrysurus</i>	X	X
				<i>Sphyræna barracuda</i>	X	X
	Mobile benthic invertivore	6	2	<i>Haemulon flavolineatum</i>	X	X
				<i>Haemulon sciurus</i>	X	
				<i>Myripristis jacobus</i>	X	
				<i>Halichoeres bivittatus</i>	X	X
				<i>Halichoeres maculipinna</i>	X	
General omnivore	2	1	<i>Abudefduf saxatilis</i>	X	X	
			<i>Abudefduf taurus</i>	X		
			<i>Ablennes hians</i>	X	X	

TABLE 2. Continued

Distance from shore (m)	Functional Feeding Group	FFG Richness		Taxa	Occurrence	
		Rocky beach habitats	Sandy beach habitats		Rocky beach habitats	Sandy beach habitats
				<i>Carcharhinus perezii</i>	X	
				<i>Eucinostomus jonesi</i>	X	
				<i>Holocentrus rufus</i>	X	
	Sand invertivore	1	0	<i>Pseudupeneus maculatus</i>	X	
	Scraper	4	4	<i>Acanthurus bohianus</i>	X	X
				<i>Acanthurus chirurgus</i>	X	
				<i>Scarus taeniopterus</i>	X	
				<i>Sparisoma aurofrenatum</i>	X	
				<i>Scartella cristata</i>		X
				<i>Bathygobius soporator</i>		X
				<i>Synodus saurus</i>		X
	Coral colonial sessile invertivore	2	1	<i>Chaetodon capistratus</i>	X	
				<i>Chaetodon striatus</i>		X
				<i>Sphoeroides testudineus</i>	X	
	Territorial algae detritivore	1	2	<i>Stegastes diencaeus</i>		X
				<i>Stegastes leucostictus</i>	X	X
	Turf grazer	1	1	<i>Acanthurus coeruleus</i>	X	X
	Group Total	29	19			
6	Diurnal planktivore	2	5	Atherinidae		X
				Engraulidae		X
				<i>Harengula humerali</i>		X
				<i>Thallasoma bifasciatum</i>	X	X
				<i>Mugil curema</i>	X	
				<i>Opistognathis macrognathus</i>		X
	Excavator eroder	1	0	<i>Sparisoma viride</i>	X	
	Macroalgae browser	2	0	<i>Archosargus rhomboidalis</i>	X	
				<i>Sparisoma radians</i>	X	
	Macrocarivore	5	5	<i>Dasyatis americana</i>		X

TABLE 2. Continued

Distance from shore (m)	Functional Feeding Group	FFG Richness		Taxa	Occurrence	
		Rocky beach habitats	Sandy beach habitats		Rocky beach habitats	Sandy beach habitats
				<i>Gerres cinereus</i>	X	X
				<i>Lutjanus apodus</i>	X	
				<i>Lutjanus synagris</i>	X	X
				<i>Ocyurus chrysurus</i>	X	X
				<i>Sphyraena barracuda</i>	X	X
	Mobile benthic invertivore	10	4	<i>Trachinotus goodei</i>	X	X
				<i>Haemulon aurolineatum</i>	X	
				<i>Haemulon flavolineatum</i>	X	X
				<i>Haemulon sciurus</i>	X	
				<i>Haemulon striatum</i>	X	
				<i>Myripristis jacobus</i>	X	
				<i>Halichoeres bivittatus</i>	X	X
				<i>Halichoeres maculipinna</i>	X	
				<i>Halichoeres radiatus</i>	X	
				<i>Scarus iserti</i>	X	X
	General omnivore	1	1	<i>Abudefduf saxatilis</i>	X	X
	Piscivore	3	2	<i>Ablennes hians</i>	X	X
				<i>Eucinostomus jonesi</i>	X	
				<i>Holocentrus rufus</i>	X	
				<i>Caranx ruber</i>		X
	Sand invertivore	1	3	<i>Pseudupeneus maculatus</i>	X	X
				<i>Bothus lunatus</i>		X
				<i>Bothus ocellatus</i>		X
	Scraper	9	4	<i>Acanthurus bohianus</i>	X	X
				<i>Acanthurus chirurgus</i>	X	
				<i>Scartella cristata</i>	X	X
				<i>Bathygobius soporator</i>	X	X
				<i>Gymnothorax funebris</i>	X	

TABLE 2. Continued

Distance from shore (m)	Functional Feeding Group	FFG Richness		Taxa	Occurrence	
		Rocky beach habitats	Sandy beach habitats		Rocky beach habitats	Sandy beach habitats
				<i>Holacanthus ciliaris</i>	X	
				<i>Scarus taeniopterus</i>	X	
				<i>Sparisoma aurofrenatum</i>	X	
				<i>Sparisoma rubripinne</i>	X	
				<i>Synodus saurus</i>		X
	Coral colonial sessile invertivore	3	2	<i>Chaetodon capistratus</i>	X	
				<i>Chaetodon striatus</i>	X	X
				<i>Sphoeroides testudineus</i>	X	X
	Territorial algae detritivore	2	3	<i>Stegastes diencaeus</i>	X	X
				<i>Stegastes leucostictus</i>	X	X
				<i>Stegastes variabilis</i>		X
	Turf grazer	1	1	<i>Acanthurus coeruleus</i>	X	X
	Group Total	40	30			
9	Diurnal planktivore	3	4	Atherinidae		X
				<i>Harengula humerali</i>		X
				<i>Cheilopogon melanurus</i>	X	
				<i>Thallasoma bifasciatum</i>	X	X
				<i>Mugil curema</i>	X	X
	Excavator eroder	1	1	<i>Sparisoma viride</i>	X	X
	Macroalgae browser	2	0	<i>Archosargus rhomboidalis</i>	X	
				<i>Sparisoma radians</i>	X	
	Macrocarivore	5	6	<i>Dasyatus americana</i>		X
				<i>Gerres cinereus</i>	X	X
				<i>Lutjanus apodus</i>	X	
				<i>Lutjanus synagris</i>	X	X
				<i>Ocyurus chrysurus</i>	X	X
				<i>Sphyraena barracuda</i>	X	X

TABLE 2. Continued

Distance from shore (m)	Functional Feeding Group	FFG Richness		Taxa	Occurrence	
		Rocky beach habitats	Sandy beach habitats		Rocky beach habitats	Sandy beach habitats
				<i>Urolophus jamaicensis</i>		X
	Mobile benthic invertivore	11	6	<i>Trachinotus goodei</i>	X	X
				<i>Haemulon aurolineatum</i>	X	
				<i>Haemulon flavolineatum</i>	X	X
				<i>Haemulon sciurus</i>	X	X
				<i>Haemulon striatum</i>	X	
				<i>Myripristis jacobus</i>	X	
				<i>Halichoeres bivittatus</i>	X	X
				<i>Halichoeres maculipinna</i>	X	X
				<i>Halichoeres radiatus</i>	X	
				<i>Lachnolaimus maximus</i>	X	
				<i>Scarus iserti</i>	X	X
	General omnivore	3	0	<i>Abudefduf saxatilis</i>	X	
				<i>Abudefduf taurus</i>	X	
				<i>Diplodus argenteus</i>	X	
	Piscivore	6	2	<i>Ablennes hians</i>	X	X
				<i>Caranx ruber</i>		X
				<i>Eucinostomus jonesi</i>	X	
				<i>Holocentrus rufus</i>	X	
				<i>Acanthostracion quadricornis</i>	X	
				<i>Nicholsina usta</i>	X	
				<i>Pareques acuminatus</i>	X	
	Sand invertivore	1	2	<i>Pseudupeneus maculatus</i>	X	X
				<i>Bothus ocellatus</i>		X
	Scraper	7	4	<i>Acanthurus bohianus</i>	X	X
				<i>Acanthurus chirurgus</i>	X	X
				<i>Gymnothorax funebris</i>	X	
				<i>Holacanthus ciliaris</i>	X	
				<i>Scarus taeniopterus</i>	X	X

TABLE 2. Continued

Distance from shore (m)	Functional Feeding Group	FFG Richness		Taxa	Occurrence	
		Rocky beach habitats	Sandy beach habitats		Rocky beach habitats	Sandy beach habitats
				<i>Sparisoma aurofrenatum</i>	X	
				<i>Sparisoma rubripinne</i>	X	X
	Coral colonial sessile invertivore	4	1	<i>Chaetodon capistratus</i>	X	
				<i>Chaetodon striatus</i>	X	
				<i>Epinephelus striatus</i>	X	
				<i>Sphoeroides testudineus</i>	X	X
	Territorial algae detritivore	2	1	<i>Stegastes diencaeus</i>	X	
				<i>Stegastes leucostictus</i>	X	X
12	Diurnal planktivore	3	2	<i>Harengula humerali</i>		X
				<i>Cheilopogon melanurus</i>	X	
				<i>Thallasoma bifasciatum</i>	X	X
				<i>Mugil curema</i>	X	
	Macroalgae browser	2	0	<i>Archosargus rhomboidalis</i>	X	
				<i>Sparisoma radians</i>	X	
	Excavator eroder	1	1	<i>Sparisoma viride</i>	X	X
	Macrocarivore	4	5	<i>Dasyatus americana</i>		X
				<i>Gerres cinereus</i>		X
				<i>Lutjanus apodus</i>	X	
				<i>Lutjanus synagris</i>	X	X
				<i>Ocyurus chrysurus</i>	X	X
				<i>Sphyræna barracuda</i>	X	X
	Mobile benthic invertivore	10	4	<i>Trachinotus goodei</i>	X	
				<i>Haemulon aurolineatum</i>	X	
				<i>Haemulon flavolineatum</i>	X	
				<i>Haemulon melanurum</i>	X	
				<i>Haemulon sciurus</i>	X	
				<i>Haemulon striatum</i>	X	
				<i>Anisotremus surinamensis</i>		X

TABLE 2. Continued

Distance from shore (m)	Functional Feeding Group	FFG Richness		Taxa	Occurrence	
		Rocky beach habitats	Sandy beach habitats		Rocky beach habitats	Sandy beach habitats
				<i>Halichoeres bivittatus</i>		X
				<i>Halichoeres maculipinna</i>		X
				<i>Myripristis jacobus</i>	X	
				<i>Halichoeres bivittatus</i>	X	
				<i>Halichoeres maculipinna</i>	X	
				<i>Lachnolaimus maximus</i>	X	
				<i>Scarus iserti</i>		X
	General omnivore	3	0	<i>Abudefduf saxatilis</i>	X	
				<i>Abudefduf taurus</i>	X	
				<i>Diplodus argenteus</i>	X	
	Piscivore	5	1	<i>Ablennes hians</i>	X	X
				<i>Holocentrus rufus</i>	X	
				<i>Acanthostracion quadricornis</i>	X	
				<i>Nicholsina usta</i>	X	
				<i>Pareques acuminatus</i>	X	
	Sand invertivore	2	1	<i>Pseudupeneus maculatus</i>	X	X
				<i>Calamus calamus</i>	X	
	Scraper	7	3	<i>Acanthurus bohianus</i>	X	X
				<i>Acanthurus chirurgus</i>	X	
				<i>Bathygobius soporator</i>	X	
				<i>Holacanthus ciliaris</i>	X	
				<i>Scarus taeniopterus</i>	X	X
				<i>Sparisoma aurofrenatum</i>	X	
				<i>Sparisoma rubripinne</i>	X	X
	Coral colonial sessile invertivore	3	0	<i>Chaetodon capistratus</i>	X	
				<i>Chaetodon striatus</i>	X	
				<i>Epinephelus striatus</i>	X	
	Territorial algae detritivore	2	1	<i>Stegastes diencaeus</i>	X	
				<i>Stegastes leucostictus</i>	X	X

TABLE 2. Continued

Distance from shore (m)	Functional Feeding Group	FFG Richness		Taxa	Occurrence	
		Rocky beach habitats	Sandy beach habitats		Rocky beach habitats	Sandy beach habitats
	Turf grazer	1	1	<i>Acanthurus coeruleus</i>	X	X
	Group Total	43	19			
15	Diurnal planktivore	3	3	Engraulidae		X
				<i>Harengula humerali</i>		X
				<i>Cheilopogon melanurus</i>	X	
				<i>Thallasoma bifasciatum</i>	X	X
				<i>Mugil curema</i>	X	
	Macroalgae browser	2	0	<i>Archosargus rhomboidalis</i>	X	
				<i>Sparisoma radians</i>	X	
	Excavator eroder	0	1	<i>Sparisoma viride</i>		X
	Macrocarivore	4	5	<i>Dasyatus americana</i>		X
				<i>Gerres cinereus</i>	X	X
				<i>Lutjanus analis</i>		X
				<i>Lutjanus apodus</i>	X	
				<i>Lutjanus synagris</i>	X	X
				<i>Ocyurus chrysurus</i>	X	X
	Mobile benthic invertivore	10	6	<i>Anisotremus surinamensis</i>		X
				<i>Trachinotus goodei</i>	X	
				<i>Haemulon aurolineatum</i>	X	
				<i>Haemulon flavolineatum</i>	X	X
				<i>Haemulon melanurum</i>	X	
				<i>Haemulon sciurus</i>	X	X
				<i>Haemulon striatum</i>	X	
				<i>Myripristis jacobus</i>	X	
				<i>Halichoeres bivittatus</i>	X	X
				<i>Halichoeres maculipinna</i>	X	X
				<i>Lachnolaimus maximus</i>	X	
				<i>Scarus iserti</i>		X

TABLE 2. Continued

Distance from shore (m)	Functional Feeding Group	FFG Richness		Taxa	Occurrence	
		Rocky beach habitats	Sandy beach habitats		Rocky beach habitats	Sandy beach habitats
	General omnivore	3	2	<i>Abudefduf saxatilis</i>	X	X
				<i>Abudefduf taurus</i>	X	
				<i>Diplodus argenteus</i>	X	
				<i>Lactophrys triqueter</i>		X
	Piscivore	3	0	<i>Ablennes hians</i>	X	
				<i>Holocentrus rufus</i>	X	
				<i>Pareques acuminatus</i>	X	
	Sand invertivore	2	0	<i>Pseudupeneus maculatus</i>	X	
				<i>Calamus calamus</i>	X	
	Scraper	5	3	<i>Acanthurus bohianus</i>	X	X
				<i>Acanthurus chirurgus</i>	X	
				<i>Holacanthus ciliaris</i>	X	
				<i>Scarus iserti</i>	X	
<i>Scarus taeniopterus</i>				X	X	
<i>Sparisoma rubripinne</i>					X	
Coral colonial sessile invertivore	2	0	<i>Chaetodon striatus</i>	X		
			<i>Epinephelus striatus</i>	X		
Territorial algae detritivore	1	1	<i>Stegastes leucostictus</i>	X	X	
Turf grazer	1	1	<i>Acanthurus coeruleus</i>	X	X	
Group Total	36	22				
20	Diurnal planktivore	2	4	Atherinidae		X
				Engraulidae		X
				<i>Harengula humerali</i>		X
				<i>Thallasoma bifasciatum</i>		X
				<i>Cheilopogon melanurus</i>	X	
				<i>Mugil curema</i>	X	
	Macroalgae browser	2	0	<i>Archosargus rhomboidalis</i>	X	
				<i>Sparisoma radians</i>	X	

TABLE 2. Continued

Distance from shore (m)	Functional Feeding Group	FFG Richness		Taxa	Occurrence	
		Rocky beach habitats	Sandy beach habitats		Rocky beach habitats	Sandy beach habitats
	Excavator eroder	0	1	<i>Sparisoma viride</i>		X
	Macrocarivore	3	4	<i>Lutjanus apodus</i>	X	X
<i>Lutjanus synagris</i>					X	
<i>Ocyurus chrysurus</i>				X	X	
<i>Sphyræna barracuda</i>				X		
<i>Urolophus jamaicensis</i>					X	
	Mobile benthic invertivore	8	5	<i>Trachinotus goodei</i>	X	
<i>Haemulon aurolineatum</i>				X		
<i>Haemulon flavolineatum</i>					X	
<i>Haemulon melanurum</i>				X		
<i>Haemulon parra</i>					X	
<i>Haemulon sciurus</i>				X	X	
<i>Haemulon striatum</i>				X		
<i>Myripristis jacobus</i>				X		
<i>Halichoeres bivittatus</i>				X	X	
	General omnivore	2	1	<i>Abudefduf saxatilis</i>	X	X
<i>Abudefduf taurus</i>				X		
	Piscivore	4	1	<i>Ablennes hians</i>	X	X
<i>Holocentrus rufus</i>				X		
<i>Nicholsina usta</i>				X		
<i>Pareques acuminatus</i>				X		
	Sand invertivore	2	1	<i>Pseudupeneus maculatus</i>	X	X
<i>Calamus calamus</i>				X		
	Scraper	6	3	<i>Acanthurus bohianus</i>	X	X
<i>Holacanthus ciliaris</i>				X		
<i>Scartella cristata</i>					X	
<i>Scarus iserti</i>				X		

TABLE 2. Continued

Distance from shore (m)	Functional Feeding Group	FFG Richness		Taxa	Occurrence	
		Rocky beach habitats	Sandy beach habitats		Rocky beach habitats	Sandy beach habitats
				<i>Scarus taeniopterus</i>	X	X
				<i>Sparisoma aurofrenatum</i>	X	
				<i>Sparisoma rubripinne</i>	X	
	Coral colonial sessile invertivore	2	0	<i>Chaetodon striatus</i>	X	
				<i>Epinephelus striatus</i>	X	
	Territorial algae detritivore	2	1	<i>Stegastes diencaeus</i>	X	
				<i>Stegastes leucostictus</i>	X	X
	Turf grazer	2	1	<i>Acanthurus coeruleus</i>	X	X
				<i>Sparisoma rubripinne</i>	X	
	Group Total	35	22			

TABLE 3. Average numbers of fish taxa observed in combined transects of nearshore rocky habitats at Francis, Great Lameshur, and Little Lameshur beaches of St. John USVI, July 2007 and July 2008. Underscored means do not differ significantly ($p=0.05$).

Distance from shore (m)	15	6	9	20	12	3	1
Avg. no. species	5.9	5.0	4.8	4.1	3.3	2.7	1.0
F=1.42; $p=0.2025$							

TABLE 4. Average numbers of fish taxa observed in combined transects at sandy habitats at Francis, Great Lameshur, and Little Lameshur beaches on St. John, USVI, July 2007 and July 2008. Underscored means do not differ significantly ($p=0.05$).

Distance from shore (m)	9	6	12	15	20	3	1
Avg. no. species	20.0	18.0	17.8	12.8	11.0	9.0	3.0
F=2.93; $p=0.0254$							

TABLE 5. Comparison of average number of species at nearshore rocky and sandy habitats at Francis, Great Lameshur and Little Lameshur beaches, St. John, USVI, July 2007 and July 2008.

Distance from Shore	Average number of species			
	Rocky habitat	Sandy habitat	F	p value
1	3.00	1.00	99.99	<0.0001
3	9.00	2.67	8.43	0.0104
6	18.00	5.00	79.85	<0.0001
9	20.00	4.89	56.38	<0.0001
12	17.75	3.27	37.54	<0.0001
15	12.80	5.89	4.93	0.0464
20	11.00	3.73	6.73	0.0159

TABLE 6. Frequency of occurrence of taxa per functional feeding group at combined nearshore rocky habitats at Francis, Great Lameshur, and Little Lameshur beaches at St. John USVI, July 2007 and July 2008.

	Distance from shore (m)						
	1	3	6	9	12	15	20
Diurnal planktivores	3	6	6	6	4	4	2
Excavators/eroders	0	0	1	1	1	0	0
Macroalgae browsers	0	0	1	1	1	1	1
Macrocarivores	1	10	17	15	8	9	3
Mobile benthic invertivores	0	12	31	33	21	17	12
General omnivores	0	5	5	7	4	8	5
Strict piscivores	1	4	7	11	7	5	5
Sand invertivores	0	3	4	4	2	2	2
Scrapers	0	4	19	20	11	9	7
Coral/colonial sessile insectivores	0	3	6	7	5	2	2
Territorial algae/detritivores	1	5	5	8	2	2	2
Turf grazers	0	2	6	6	4	4	2
Total	6	54	108	119	70	63	43

TABLE 7. Frequency of occurrence of taxa per functional feeding group from combined nearshore sandy habitats at Francis, Great Lameshur, and Little Lameshur beaches at St. John USVI, July 2007 and July 2008.

Functional feeding group	Distance from shore (m)						
	1	3	6	9	12	15	20
Diurnal planktivores	2	3	8	7	4	5	5
Excavators/eroders	0	0	0	2	1	2	1
Macrocarivores	0	7	12	17	8	8	6
Mobile benthic invertivores	0	8	11	15	9	14	11
General omnivores	0	1	1	0	0	3	2
Strict piscivores	0	1	8	4	1	0	1
Sand invertivores	0	0	7	7	4	4	3
Scrapers	0	4	6	9	6	9	6
Coral/colonial sessile insectivores	0	1	4	1	0	0	0
Territorial algae/detritivores	0	4	5	4	2	4	7
Turf grazers	0	3	4	4	1	4	3
Total	2	32	66	70	36	53	45

TABLE 8. Comparison of taxa richness, diversity (H), and evenness of functional feeding groups between rocky and sandy habitats at combined Little Lameshur, Francis Beach, and Great Lameshur, St. John USVI, July 2007 and July 2008.

		Distance from shore (m)					
		3.00	6.00	9.00	12.00	15.00	20.00
Richness	Rocky	7.00	10.00	10.00	8.67	8.00	6.67
	Sandy	5.33	8.33	7.33	5.67	6.67	7.33
	t value	5.57	16.89	11.4	6.14	10.26	6.22
	p>t	0.0020	<.0001	<.0001	0.0017	0.0002	0.0016
H Index	Rocky	1.84	2.04	2.05	1.91	1.90	1.53
	Sandy	1.43	2.02	1.82	1.55	1.77	1.86
	t value	8.05	60.02	26.46	10.23	18.96	7.82
	p>t	0.0005	<.0001	<.0001	0.0002	<.0001	0.0005
Evenness	Rocky	0.9764	0.8896	0.8927	0.8939	0.9171	0.9061
	Sandy	0.9539	0.9551	0.9226	0.9309	0.9606	0.9425
	t value	60.03	53.53	89.59	67.62	62.84	77.93
	p>t	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001