Reef Fish Community Structure in Bocas del Toro (Caribbean, Panama): Gradients in Habitat Complexity and Exposure

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ABSTRACT.—We compared the community-structure of reef-fish over different spatial scales, levels of exposure, and physical complexity in 12 study zones of Bocas del Toro, Panama. Two hundred and eighty-eight visual censuses were conducted on 48 benthic transects from April to September 2002. Substrate coverage and surface complexity was also recorded. We found 128 fish species in 38 families with increasing species richness from sheltered to expose and from low-complexity to intermediate and high-complexity zones. Only 7% of the species occurred in all zones. Gobies and pomacentrids were most abundant in sheltered areas and labrids at exposed zones. Eleven species showed significant size-segregations between zones, suggesting ontogenic movements, with smaller sizes in low-complexity zones, and larger-sizes in intermediate to high complexity areas. Species-richness and diversity are high in three of the four exposed zones and in the main areas of massive-coral reefs and significantly correlate with certain types of complex substrates. Highly mobile fish were more abundant in exposed rocky zones while sedentary fish were more abundant in sheltered massive and foliaceous corals zones. Towards the most exposed areas, the number of mobile invertebrate-feeding fish species greatly increased, while territorial herbivores increased in sheltered zones. Roving herbivores (scarids and acanthurids) showed lower frequency than territorial herbivores in all zones. Demersal zooplankton feeders were common in sheltered areas and oceanic planktivores in exposed areas. Omnivores were more abundant in zones of rubble and sand. Carnivores were less frequent, but contribute to the majority of species. We concluded that the species' richness in Bocas del Toro relates to the structural complexity of the substrate rather than substrate type. While some species change their preferred habitat during ontogeny, general species diversity increased with habitat complexity. This increase was more pronounced in exposed zones. It seem that water current strength and waves, which select for swimming capacity, play an important but still little understood role in the organization of fish assemblages in rocky and coral reefs.

KEYWORDS.—Fish diversity, distribution, fish mobility, trophic groups, exposure level, lagoonal system, Mesoamerican Caribbean

INTRODUCTION

It has been widely stated that there are geographic gradients in the richness of fish species, corals and other coral reef biota, with a general decrease in diversity with increasing latitude and distance from the Indo-Philippine 'centre' (Goldman and Talbot 1976; Veron 1995). In the Atlantic Ocean, the Caribbean is thought the diversity centre for both fishes and corals (Briggs 1995; Veron 1995; Floeter and Gasparini 2000). The present study focuses on Bocas del Toro, which forms part of the Southern Caribbean biogeographic province. For this area, and the Caribbean Mesoamerican region in general, only a few studies exist that address variation in the community-structure of reef-fishes (Sierra and García 1996; Clifton and Clifton 1998), and most of these were conducted along Caribbean islands away from the mainland (McGehee 1994; McKenna 1997). Generally, species composition varies among different habitats (Talbot and Goldman 1972; McGehee 1994) and it appears that a strong taxonomic division between reef and non-reef faunas is difficult. "Reef fishes" may thus be characteristic of—but not restricted to—coral reefs (Robertson 1998; Bellwood

1998). Support for this assertion can be found in different geographical regions, such as the south-western Atlantic, where the most diverse fish faunas are along rocky shores with low coral coverage (Floeter et al. 2001).

Studies concerning reef fish have focused almost exclusively on coral reefs, not including a wide spectrum of reef habitats (Robertson 1998). They usually compare either diverse living coral-reef areas or rocky shores. The structural complexity of a habitat is very important for the community organization, since it provides physical structure for juvenile and adult animals (Jones 1988; Beck 1997 1998); it plays an important role in the regulation of foraging patterns (Dolmer 1998; Erlandsson et al. 1999) and predation (Hixon and Beets 1993); it also plays an important role in habitat selection (Levin and Grimes 2002), and in some cases relaxes competition (Diehl 1988). The role of complexity seems clear for most researchers, but whether its difference among areas is due to the degree of coverage of living coral or other habitat characteristics should be studied on a spatial scale that includes different habitats and levels of exposure to waves and currents. The presence of currents may affect larval dispersal and retention, thus influencing the populations' connectivity (Cowen 2002). The relative contribution of population growth, mortality, food requirements, metabolic level to fitness, as well as the role of habitat structure and selection, requires further investigation (Jones and McCormick 2002), In this context, *edges* of habitats have often been severely under sampled (Sagarin and Gaines 2002). Swimming ability and trophic behaviour are also important properties of species that may influence community organization. More studies are necessary in this field.

We compared the community-structure of reef-fish in the Bocas del Toro region of the Tropical western Atlantic, which exhibits one of the highest diversity and abundance of corals in shallow Caribbean waters (Guzmán and Guevara 1998a,b 1999). This Mesoamerican or "isthmian" Caribbean is a peculiar region due to the many geological changes it has been subjected to, including the emergence of the Isthmus of Panama.

The study aimed to characterize fish assemblages (including taxonomical composition, abundance and species richness) along spatial scales and gradients of substrate complexity to determine the relative importance of the physical structure provided by corals, rocks and benthic sessile substrate-building organisms. We also determined characteristics such as mobility, home range, size, territoriality, and feeding behaviour responsible for the selection of habitats by certain species and/or guilds along gradients of wave exposure, reef type (i.e., Coral reef vs. rocky reef) and general substrate complexity.

MATERIALS AND METHODS

Study site

The study was conducted from April to September 2002 in sheltered areas of Almirante Bay and the exposed areas around Isla Bastimentos at the Province of Bocas del Toro (8°30′09°40′N, 82°56′081°08′W), (Fig. 1).

Intense rain and irregular seasonal patterns characterise Bocas del Toro. The most important coastal current comes from an easterly direction of Nicaragua and Costa Rica (Greb et al. 1996). Waves and currents have a strong effect outside of the archipelago, but the major islands act as a barrier, decreasing wind-strength, wave-height, and tidal amplitude for the inner water bodies (Bahía de Almirante and Laguna de Chiriquí). A sheltered semi-lagoonal system with tidal amplitudes < 0.5 m is created, which supports mangrove forests. Changes in oceanic conditions of the southern Caribbean during the late Miocene, due to the progressive constriction of the Atlantic-Pacific seaway weakened the westward circulation and the southern Caribbean flow (Collins et al. 1996). All these changes resulted in a well-defined semi-lagoonal system that is connected to the southern reef areas of the Caribbean from Costa Rica (Cortés 1984).
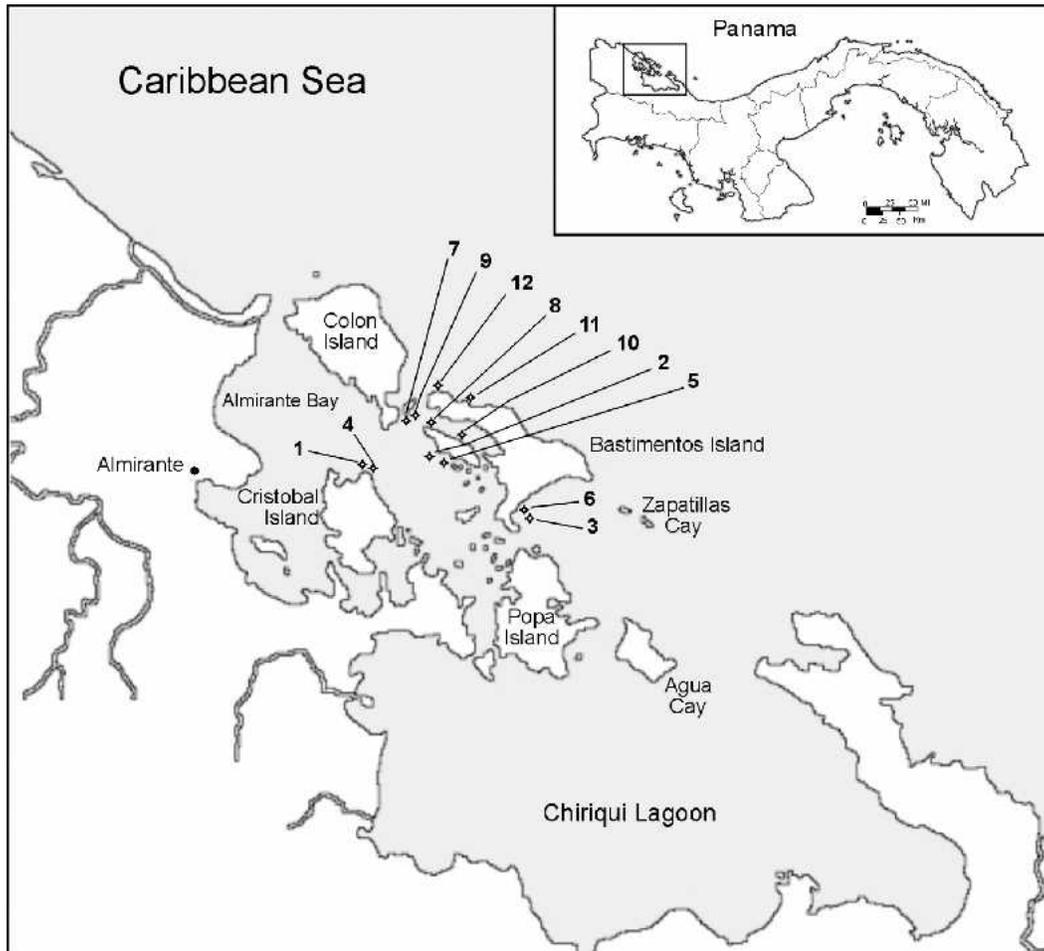
FIG. 1. Sampling zones in Bocas del Toro, Caribbean. 1: North east of Cristóbal Island; 2: South of Solarte Island; 3: Crawl Key, west side of Bastimentos Island; 4: Northeast of Cristóbal Island; 5: South of Solarte Island; 6: Crawl Key; 7: Carenero Island; 8: Hospital point, northeast of Solarte Island; 9: Carenero Key; 10: Northwest of Solarte Island; 11: Wild Cane Key, north of Bastimentos Island; 12: Bastimentos Point, east of Isla Bastimentos.

The selection of study sites was based on a preliminary-survey that identified areas with different but nevertheless characteristic habitats of the region. From this survey, 12 characteristic zones were classified in terms of depth, substrate type, topography and cover. Within each of the 12 zones, four benthic 30 m transects were set up parallel to the shore at approximately the same depth. Substrate coverage and surface complexity was estimated using a link-chain methodology (CARICOMP 2001; Rogers et al. 1994). The benthic surface measures were taken along the chain that would lay limp following the surface contour of the substrate. In this way the structural complexity of the substrate was estimated as the ratio between the length of the chain laid over the substrate and the direct linear length from the beginning to the end of each transect. The number of links outlining the surface of the substrate was counted, noting the kind of substrate under each segment of the chain; the length of the contour for each portion was then estimated at 1.6 cm per chain-link.

A detailed description of the benthic regions is in Guzmán and Guevara (1998a,b

1999). We classified the zones in ascending order of complexity (1 to 12) along with the following general description (Fig. 2):

Zones of sand and rubble SRU (1-2): Found in deeper areas adjacent to patches of the branching coral *Porites furcata*.

Zones of turf-algae and dead branching coral TA (3): A mixture of eroded skeletons of foliaceous and branching corals, with a dense cover of different species of turf-algae. These zones were found below the exposed reef-slope of fire-coral zones.

Zones of madreporic branching coral BC (4-5): Patchy zones dominated by the finger-like coral *Porites furcata*.

Zones of fire-coral FC (6): Continuous shallow zones (reef flat) exposed to wave influence and characterised by the presence of the fire coral *Millepora complanata*, macroalgae and other benthic components.

Zones of foliaceous coral FOLI (7-8): Sheltered deeper reefs covered with living and dead colonies of the scleractinean coral *Agaricia tenuifolia*.

Zones of massive coral MC (9-10): Coral-reef zones separated by sand, with a mix-

ture of living and dead massive coral of different genera including *Montastraea cavernosa*, *Siderastrea siderea;* also erect sponges and sand.

Zones of massive volcanic rocks: Not common in Bocas del Toro and virtually absent in sheltered areas (pers. obs.). This kind of habitat was found on a single deeper profile (11) and in a single shallow one (12). It has a component of sessile organisms (e.g., encrusting sponges and algae) that tend to predominate in areas of high disturbance and strong currents and waves (Dethier 1994; Steneck and Dethier 1994).

The species and abundance of fish was assessed using standard methodology for underwater visual-survey with SCUBA diving equipment (English et al. 1994; Khalaf and Kochzius 2002; McKenna 1997). The fixed benthic transects (30 * 5 m) used for the study of the benthos were also used for the fish census. Monthly sampling was conducted at all transects (six census per transect), amounting to 288 on 48 benthic transects. Two to three observers swam along the transects, recording data for fishes (including small cryptic individuals)
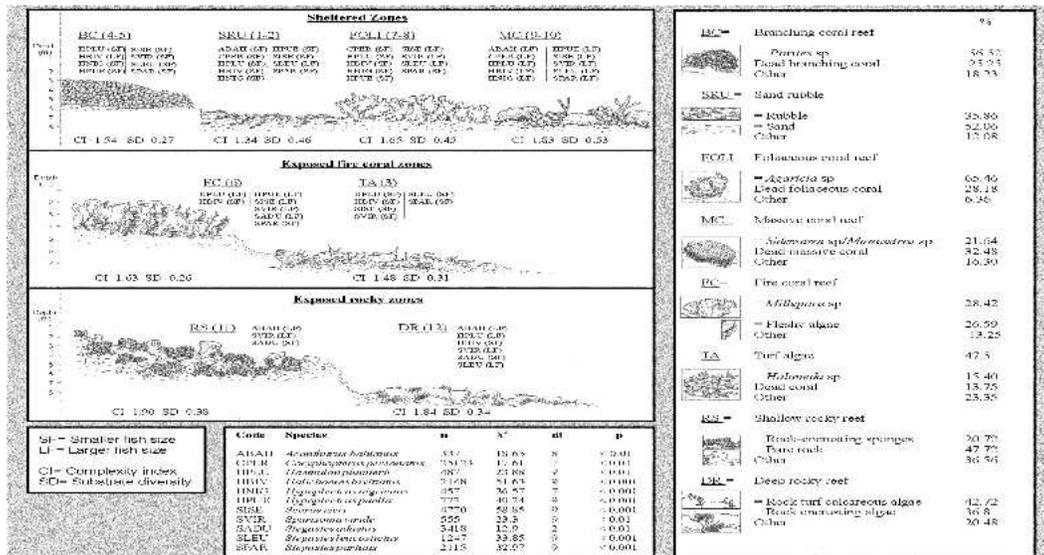

FIG. 2. Summary of habitat structure variables and results of the frequency analysis (X^2) to test the differences in size distribution of species and habitat type, only the species that had significant differences of small and larger individuals are showed.

encountered within 2.5 m on both sides and 5 m above. The standard length (SL) of the fishes was estimated to the nearest centimetre with a PVC ruler. From these data, abundance (indiv./150 m^2) and Shannon-Wiener diversity (H′) were calculated based on relative abundance (Pielou 1975).

Each species was included in one of three mobility /home range size categories, as applied by Floeter et al. 2004: Category 1 represents high mobility, including wide horizontal displacement species (e.g., roving herbivores, mullids). Category 2 is represented by relatively sedentary and demersal species in close association with the reef substrate (e.g., serranids, haemulids, chaetodontids). Category 3 includes species with a small home range and a site attachment also expressed by territorial behaviour (e.g., gobies, damselfishes).

Fish species were trophically classified following Ferreira et al. (2004) and Jones et al (1991) as: roving herbivores: fish that feed on detritus, turf algae and macroalgae (scarids and acanthurids); territorial herbivores: fish that feed on farmed turf-algae within their territories; mobile-invertebrate feeders: fish that feed primarily on crabs, molluscs and other benthic mobile invertebrates on hard and soft substrates; sessile-invertebrate feeders: fish that eat sessile benthic invertebrates; piscivores: fishes that prey on living fishes; carnivores: fish that feed on mobile benthic organisms and also fishes; planktivores: fish that consume primarily macro and micro-zooplankton; omnivores: fishes that feed on a variety of organisms, including both animal and plant material.

We used the Simpson's diversity index to estimate the diversity of organic and inorganic habitat categories (Ferreira et al. 2001). The index ranges from zero (highest diversity) to one (monotony). An index value of one indicates coverage by a single kind of substrate. Since much of the data on physical and biological parameters may not meet the criteria for normality and homogeneity of variances, parametric one-way ANOVA or non-parametric Kruskall-Wallis tests (Kruskall-Wallis) were applied to the data after testing for normality. Study sites were then compared for differ-

ences in physical conditions (substrate diversity), fish density, mobility pattern groups and index of diversity (H′) of fish assemblages (Zar 1996). An additional Student-Newman-Keuls (SNK) test of multiple-comparisons of means was applied as a *post-hoc* test (Zar 1996). The relationships between diversity indices, species density, and physical parameters were examined using Spearman rank-correlation (Siegel 1970; Peet 1974; Sokal and Rohlf 1980; Zar 1996). Association between the most abundant species, mobility pattern groups and their relationship with the habitat was examined using Canonical Correspondence Analysis (CCA) (Ter Braak and Verdonschot 1995). For this CCA analysis a value for the degree of exposure (score 0 to 4) was determined by general field observations. Differences in size distribution of all species and habitat types were examined based on length frequencies and applying chi-square analysis (χ^2) to the size groups.

Fish abundance for different zones were pooled and visually presented in a rank-order of species according to their corresponding log numbers to easily visualize the species richness and relative importance of live coral coverage and low coral coverage substrates vs. complexity (zone number) at the different study zones (Wolff and Alarcón 1993).

RESULTS

The One-Way ANOVA (Table 1) showed significant differences of the Simpson's diversity index between some zones. It ranged close to zero (highest substrate diversity) at many of the exposed zones, especially fire corals and rocky reef, and it was close to one (monotony) in the sheltered zones that had similar index values (Fig. 2).

One hundred twenty eight fish species in 38 families were found (Appendix). The total number of fish species increased from sheltered to exposed zones. The number of genera and species found at all locations was not equal; 63% of the genera were restricted to certain zones, and only 7% of the species occurred in all zones. The number

TABLE 1. Results of parametric (One way ANOVA: F, MS) and non-parametric (Kruskal Wallis, H) ANOVA and multiple comparisons (Student Neumann Keuls, SNK) for diversity comparisons (fish and habitat), and mobility groups between study zones in Bocas del Toro. ND = Normal distribution data, NND = Non normal distribution data.

	H	Df	F	MS	p	Multiple comparison (SNK)
Substratum diversity						
(Simpson's diversity index)	ND	11	7.90	0.04	<0.001	Other zones < 8 = 7 = 5 = 4 = 2 = 1
Fish diversity (H')	ND	11	9.94	0.065	<0.001	12 = 11 = 6 > other zones
Fishes/census	36.52	11	NND	NND	<0.001	5 = 2 = 1 > other zones
Category 1	40.89	11	NND	NND	<0.001	12 > other zones
Category 2	42.57	11	NND	NND	<0.001	12 = 11 = 2 = 1 > other zones
Category 3	32.62	11	NND	NND	<0.001	10 = 9 = 8 = 2 = 1 > other zones

of species per genus increased from low-complexity to intermediate and high-complexity zones in the entire region. Regardless of their densities, many of the genera and species in the families (e.g., Blennidae, Labridae) and species in the genera (e.g., *Halichoeres* spp.) were not overlapping. They showed marked differences in distribution between protected and exposed zones (Appendix).

In the size frequency analysis 27 species were abundant enough to allow segregation by size; all these species were habitat-representative and 11 of them show significant size-segregation between different zones (Fig. 2). Non-territorial species such as *Scarus iseri*, *Halichoeres bivittatus*, *Acanthurus bahianus*, *Sparisoma viride*, and *Haemulon plumierii*, had smaller sizes (juveniles and pre-adults) in low-complexity zones such as sand rubble and turf algae; while larger sizes increase proportionally in zones of intermediate and high-complexity such as those of massive and fire coral, and also in some cases in complex exposed rocky zones. The genus *Hypoplectrus* showed a similar pattern but larger individuals were scarce at any of the exposed zones. Sedentary species such as *Coryphopterus personatus* and *Stegastes partitus* were also present at smaller sizes on sand-rubble areas and at larger sizes in zones of intermediate complexity such as those of branching, foliaceous, and massive coral. Individuals of *Stegastes adustus* were smaller at all rocky zones and larger at fire-coral locations. Individuals of *Stegastes leucostictus* had smaller sizes at zones of branching coral and turf-algae, but the

larger sizes were found in zones of different levels of complexity and according to no discernible pattern (Fig. 2).

Gobies and pomacentrids were the most abundant families. The goby *Coryphopterus personatus* was the most common species in sheltered zones along with some labrids, such as *Halichoeres bivittatus*, the scarid *Scarus iseri*, the pomacentrid *Stegastes planifrons*, the serranid *Serranus tortugarum* and the haemulid *Haemulon plumierii* (Fig. 3). On the other hand, the species *Thalassoma bifasciatum*, *Chromis multilineata*, *Stegastes adustus* along with some acanthurids were common at exposed zones (Fig. 4).

As revealed by the results of Canonical Correspondence Analysis (CCA), (Table 2, 3 and Fig. 5), the association between fish and environmental variables for the 12 study zones show (at the right side of Axis 2) a gradient of exposure. Most exposed zones were associated with rock-encrusting red algae and fire coral (Zone 6, 1.22 m; Zone 11, 8.15 m; Zone 12, 3.88 m). Fishes associated with this axis were: *Thalassoma bifasciatum* (TLUC), *Halichoeres maculipinna* (HMAC), *Chromis multilineata* (CMUL), *Stegastes adustus* (SADU), the acanthurids *Acanthurus bahianus* (ABAH) and *Acanthurus chirurgus* (ACHI) which had a closer association with this group at exposed zones. The positive side of Axis 1 showed sheltered zones with branching corals (Zones 4 and 5, *Porites furcata*, 2.5 m) and zones with foliaceous corals (Zones 7 and 8, *Agaricia tenuifolia* 6.93 m). Here *Stegastes planifrons* (SPLA) and *Scarus iseri* (SISE) predominated, along with *Hypoplectrus* spp. (HPUE, HNIG), and some other species. Zone 3

Sheltered zones
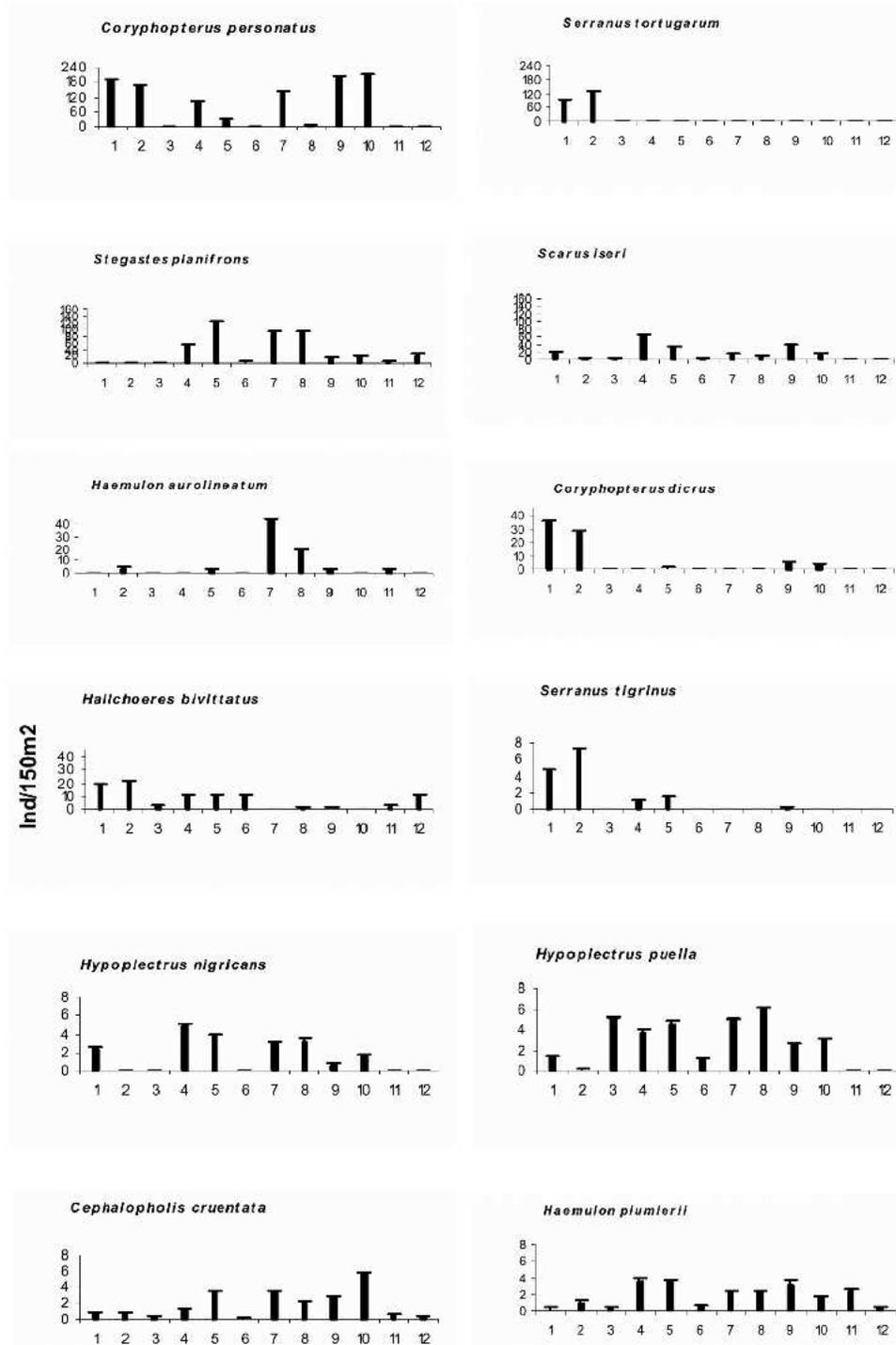
FIG. 3. Density (Ind/150 m² ± SE) for the most abundant species found in sheltered zones (1, 2, 4, 5, 7, 8, 9, and 10) in Bocas del Toro, Panama.
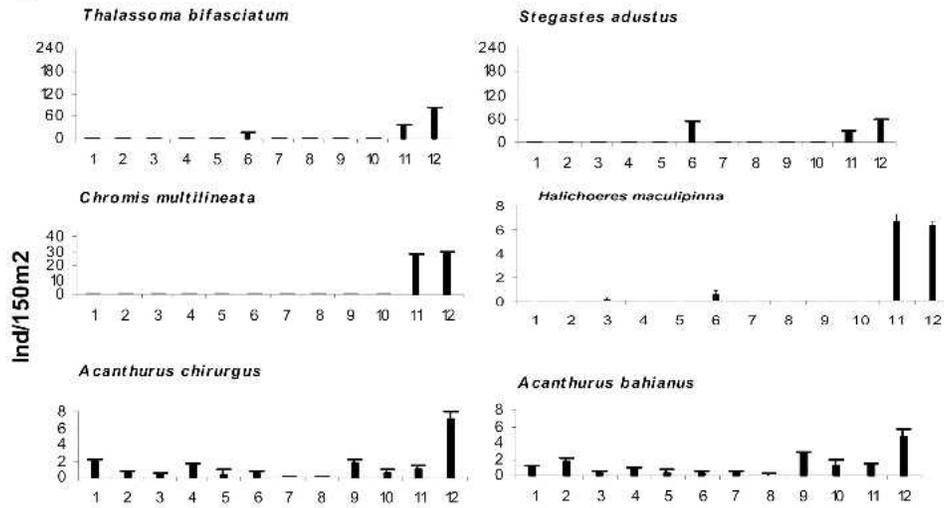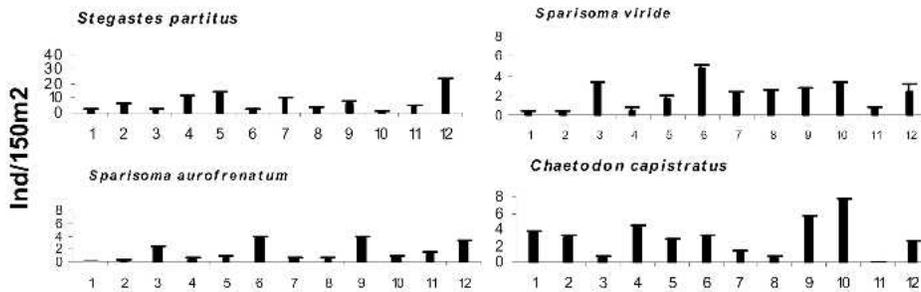
Exposed zones

FIG. 4. Density (Ind/150 m² ± SE) for the most abundant species found at exposed zones (3, 6, 11, 12) and most of the zones in Bocas del Toro, Panama.

(deeper exposed zone 6.3 m) shows similar habitat composition than 4 and 5, except for the lack of living coral coverage, and had a similar fish fauna as zones 4, 5, 7, and 8. The negative part of Axis 1 shows sand-rubble areas (Zones 1 and 2, 6.36 m), which associate with *Serranus tortugarum* (STOR), *Serranus tigrinus* (STIG), the goby *Coryphopterus dycrus* (CDIC) and the labrid *Halichoeres bivittatus* (HBIV). A fourth group closer to the centre of the ordination diagram is comprised by species found in all study zones: the pomacentrid *Stegastes partitus* (SPAR), the scarids *Sparisoma viride* (SVIR), *Sparisoma aurofrenatum* (SAUR) and the chaetodontid *Chaetodon capistratus.*

The results of One-Way ANOVA and multiple comparisons (Student-Newman Keuls [SNK]) for fish parameters show significant differences in the Shannon-Wiener index (Ĥ) between some zones (Table 1). Fish diversity had higher and similar values in three of the four exposed zones, including the rocky deeper zone (11), followed by shallow rocky zone (12), and shallow fire-coral zone (6). All other zones had a lower diversity.

These differences are appreciated in more detail in the log-series model in Fig. 6. The flatness of the line (greatest evenness) as well as its intersection with the x axis (Species richness) was greatest in the more

TABLE 2. Dominant species. O = Omnivore; C = Carnivore; P = Piscivore; MI = Mobile Invertebrate feeder; SI = Sessile Invertebrate feeder; PL = Planktivore; RH = Roving Herbivore; TH = Territorial Herbivore.

Code	Species	Family	Trophic group
ABAH	*Acanthurus bahianus*	ACANTHURIDAE	RH
ACHI	*Acanthurus chirurgus*	ACANTHURIDAE	RH
CCAP	*Chaetodon capistratus*	CHAETODONTIDAE	SI
CDIC	*Coryphopterus dicrus*	GOBIIDAE	O
CMUL	*Chromis multilineata*	POMACENTRIDAE	PL
CPER	*Coryphopterus personatus*	GOBIIDAE	PL
CCRU	*Cephalopholis cruentata*	SERRANIDAE	C
HAUR	*Haemulon aurolineatum*	HAEMULIDAE	C
HBIV	*Halichoeres bivittatus*	LABRIDAE	MI
HMAC	*Halichoeres maculipinna*	LABRIDAE	MI
HNIG	*Hypoplectrus nigricans*	SERRANIDAE	C
HPLU	*Haemulon plumierii*	HAEMULIDAE	C
HPUE	*Hypoplectrus puella*	SERRANIDAE	C
SADU	*Stegastes adustus*	POMACENTRIDAE	TH
SAUR	*Sparisoma aurofrenatum*	SCARIDAE	RH
SISE	*Scarus iseri*	SCARIDAE	RH
SPAR	*Stegastes partitus*	POMACENTRIDAE	TH
SPLA	*Stegastes planifrons*	POMACENTRIDAE	TH
STIG	*Serranus tigrinus*	SERRANIDAE	C
STOR	*Serranus tortugarum*	SERRANIDAE	PL
SVIR	*Sparisoma viride*	SCARIDAE	RH
TBIF	*Thalassoma bifasciatum*	LABRIDAE	PL

TABLE 3. Canonical Correspondance Analysis. VCP = Variance in cumulative percentage. SEV = Sums of eigenvalues. SACCA = Species association (Fig. 5). MCCA = Mobility groups (Fig. 8).

	SACCA			MCCA	
VCP	41.45	66.30	75.50	62.30	100.0
SEV	0.78	0.46	0.17	0.11	0.07

complex zones 6, 9, 10, 11, and 12, independent of their coral coverage. The lines of zones 1 to 5, 7, and 8 that had predominance of a single type of substrate (e.g., rubble, branching or foliaceous corals) had a higher slope and lower regression coefficient, indicative of a higher dominance within the assemblage and of a less diverse community respectively. All outlier points above the lines (omitted in Fig. 6 for better graphic visualization) correspond to the low and medium complexity sheltered zones and represent the dominant species of pomacentrids, gobiids and serranids (dwarf basses, *Serranus* sp.). More species were in areas with complex massive coral and rocky reef.

The non-parametric ANOVA (Kruskal Wallis) shows that fish abundance differs significantly between zones. Zones of rubble (1 and 2) and branching corals (5) had the higher fish abundance (Table 1, see Fig. 3 and 4 for most abundant species).

The Spearman rank-correlation analysis (Fig. 7) shows significant positive correlation between species-richness and index of diversity with habitat complexity and certain types of substrates such as rocks with encrusting red algae, dead and living massive coral, turf calcareous algae, rock-encrusting sponges. An inverse correlation was significant for species richness and fish diversity with the Simpson's index. Monotony (single type of substrate, value close to 1) was related to a less diverse fish community structure. Inverse correlations were also found with diversity parameters and dead and living branching coral, dead foliaceous coral, and turf-algae, and (on a lower level) for living foliaceous coral, calcareous algae, and rubble.

Fish abundance (indiv./census) seem positively correlated only with substrates like dead massive coral, sand, and erect sponges (Fig. 7), due to the high abundance

FIG. 5. Canonical Correspondence Analysis (CCA) for fish abundance vs. percentage of substrate coverage and environmental variables associated to respective zones (numbers) in Bocas del Toro, Panama. Species codes are shown on Table 2.

of the gobiid *Coryphopterus personatus* and the serranid *Serranus tortugarum*. Total fish-abundance was inversely correlated with hard substrates as living and dead branching coral, fire-coral with fleshy and turf brown algae (Fig. 7).

As seen in Table 1, the rocky shallow zone (12) had more fishes of high horizon-tal and vertical mobility (Category 1). Rela-tively sedentary species (Category 2) had similar abundance in rubble-sheltered zones (1 and 2) and exposed rocky reef (11 and 12). Site attached species (Category 3) were more represented in rubble (1 and 2), foliaceous (7 and 8) and massive coral zones (9 and 10). This association of mobil-

Shallow living corals

Deep living corals

Low coral coverage
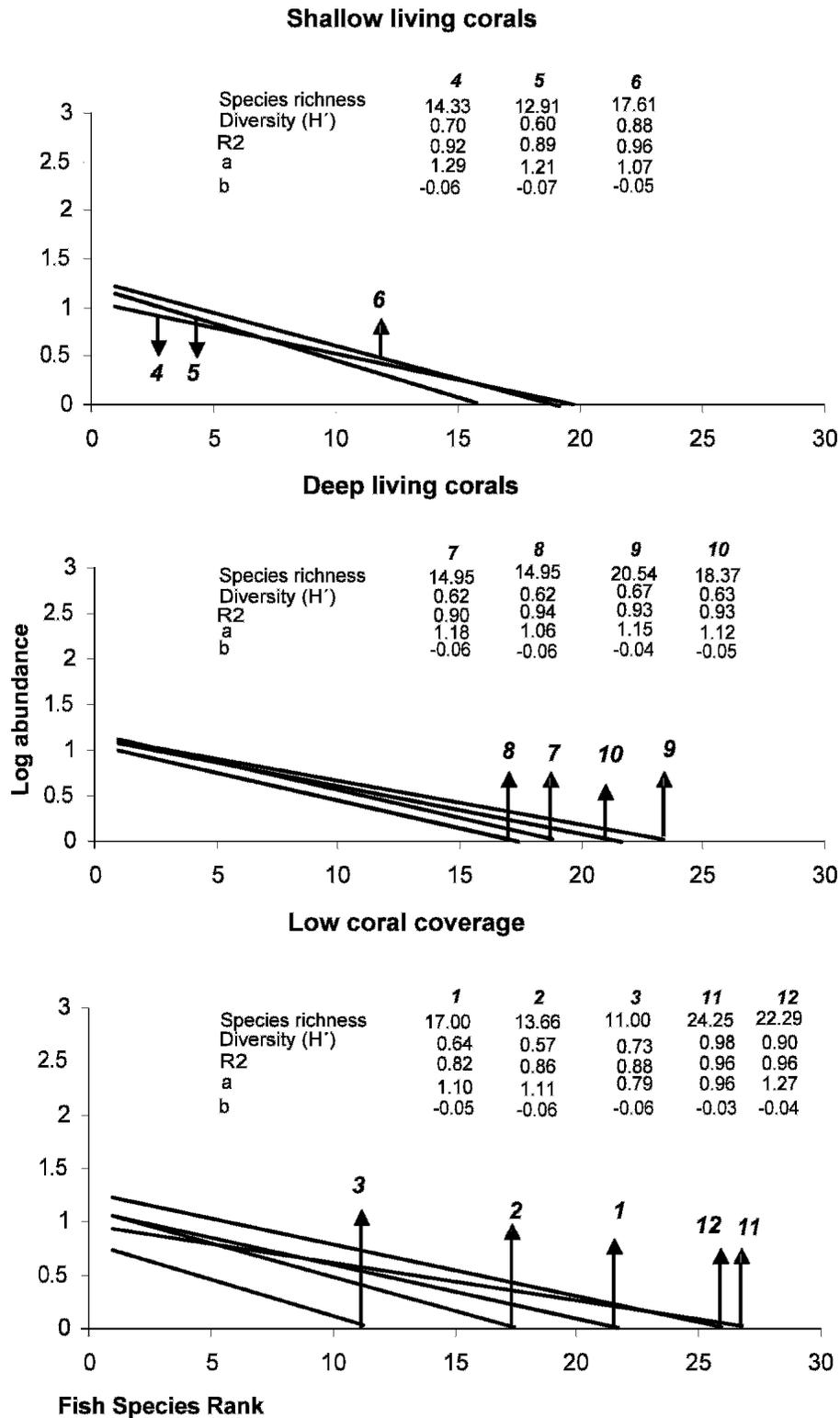
Fish Species Rank

FIG. 6. Species Rank vs. log-abundance (log-series model). Shallow living coral (1.22-3.05 m); Deep living coral (5.9-7.9 m); Low coral coverage (3.8-8.15 m). Outlier points omitted for better graphic visualization.
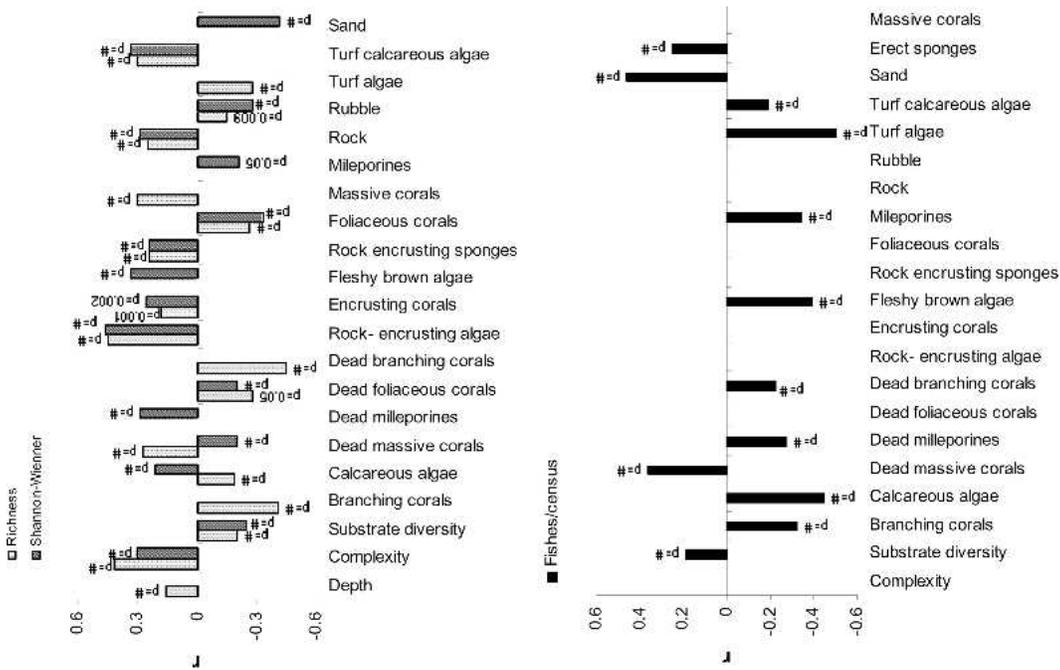
FIG. 7. Spearman rank correlations between fish community structure and habitat variables; $n = 288$, $\# = p < 0.0001$.

ity groups or categories with certain habitat attributes and zones was revealed by the CCA-Analysis (12 zones; all species included Table 3; Appendix and Fig. 8), which shows the environmental variables by arrows and the Categories in the different zones in a single diagram. At the right (positive) side of Axis 2 a gradient of exposure is found (clockwise) with most exposed zones (11 and 12) associated with a habitat of rock-encrusting red algae. Fishes in Category 1 (high mobility species) were associated with this axis mainly by the presence of the planktivorous *Chromis multilineata*, *Thalassoma bifasciatum* and acanthurids. The area between the negative side of Axis 2 and negative side of Axis 1 shows, in an anti-clockwise direction, the sheltered zones with foliaceous corals (*Agaricia tenuifolia*) and the presence of massive and shallow branching corals reef (*Porites furcata*). Here, the Category 3 (site attached species) is mostly represented by *Coryphopterus personatus* and *Stegastes planifrons*. Category 2 (relatively sedentary species) in rubble-sheltered zones is mostly

represented by *Serranus tortugarum* and this category is also related to exposed zones (11 and 12) where relatively sedentary families were more diverse (e.g., Serranidae, Balistidae) (Fig. 3, 4 and 8, Appendix).

As compared to sheltered areas, in most exposed and complex areas, such as Punta Bastimentos (12), Wild Cane (11), and Crawl Cay (6), fish of specific trophic groups (e.g., mobile-invertebrate feeders) increase in abundance and species numbers Herbivores accounted for 77% of the relative fish abundance in Bocas del Toro with a predominance of territorial herbivores in almost all zones. Their frequency increased toward sheltered zones; however roving herbivores (scarids and acanthurids) were less frequent in all zones.

Along with herbivores, demersal zooplankton feeders (in sheltered areas) and planktivores that use a larger part of the water column (at exposed zones) were common trophic groups in Bocas del Toro, but of low species numbers. Omnivores were more abundant in zones of rubble and sand; mobile-invertebrate feeders increased
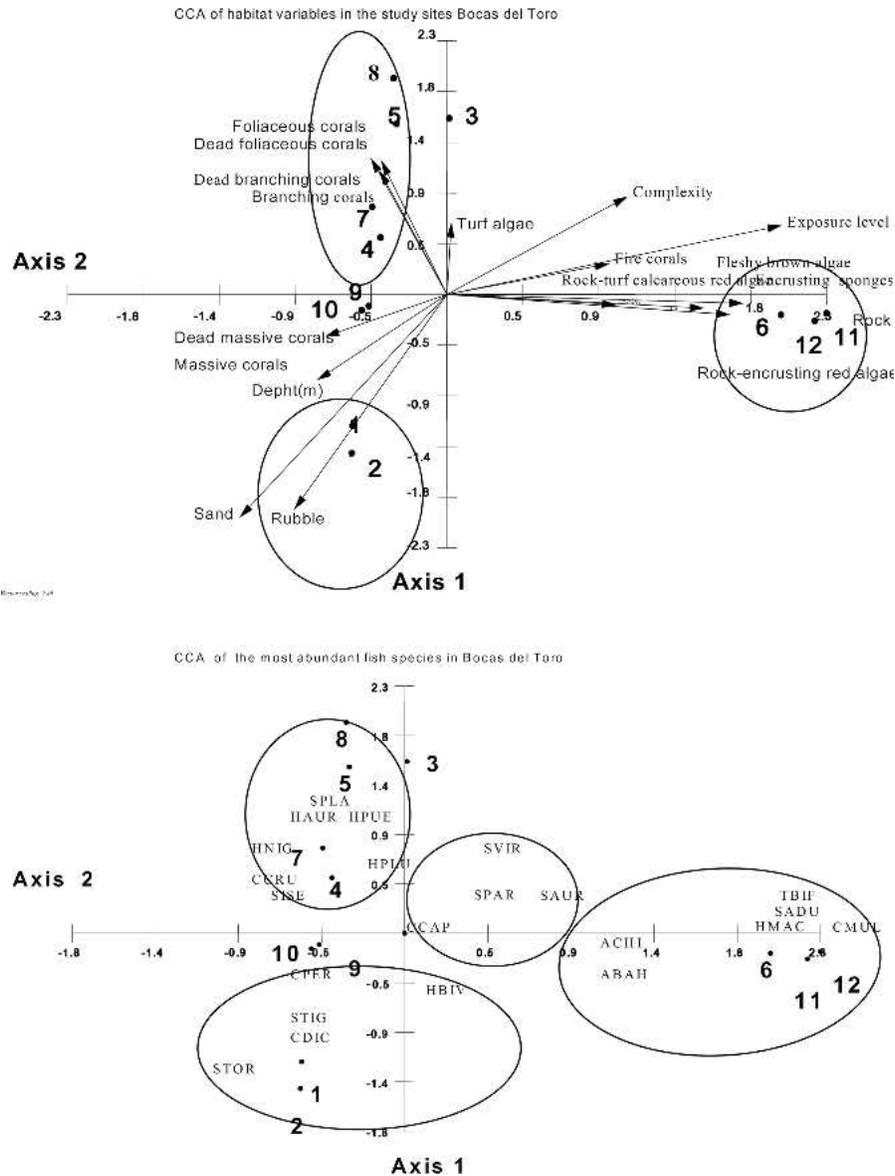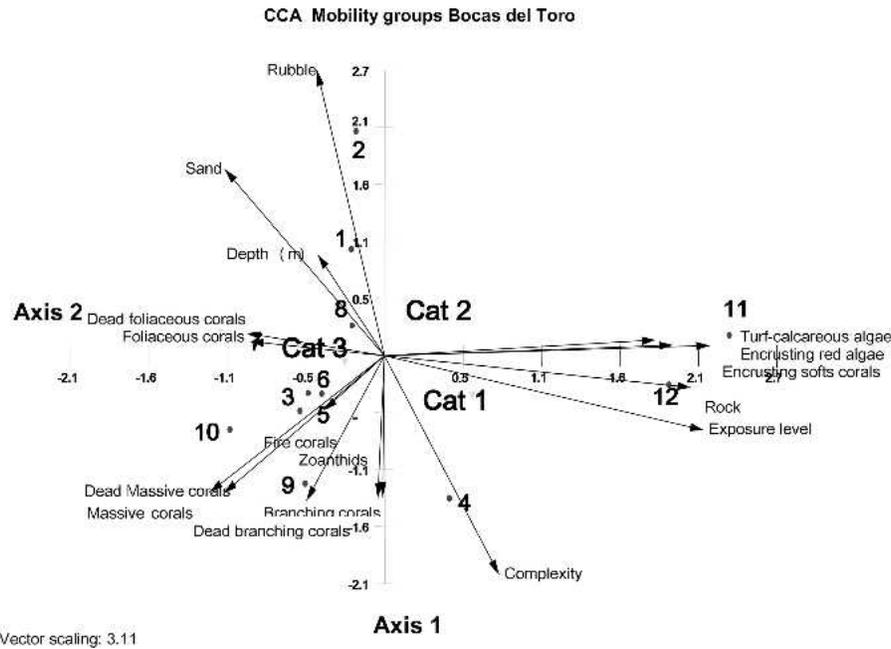
FIG. 8. Canonical Correspondence Analysis (CCA) mobility groups (categories) vs. percentage of substrate coverage and environmental variables associated to respective zone (numbers) in Bocas del Toro, Panama.

in relative abundance and diversity from sheltered to exposed zones.

Carnivores are less frequent compared to the other mentioned trophic groups, but included the majority of species. Their species number did not vary significantly among zones. Sessile-invertebrate feeders and piscivores were represented by few species and were found in low numbers only (Fig. 7).

DISCUSSION

Along with other factors, the distribution pattern of a species varies with ontogenetic morphological changes and shifts in habitat requirements (García-Charton and Pérez-Ruzafa 2001; Nagelkerken et al. 2000a,b). Some species ontogenetic movement between habitats may be directed towards more complex habitats and related to swimming ability of post recruits (see respective section). Few studies have been conducted in this field, but Aburto-Oropeza, and Balart (2001) found spatial variation and size-discrimination for eight of the most abundant species in the Gulf of California. The smaller individuals on low-complexity substrates may be able to hide while predators and other large fish may lack retreats. We consider these patterns also to play an important role for the organization of reef fish assemblage in Bocas del Toro.

Our results indicate that in many fish families species numbers increased toward more complex zones and densities of specialized feeders (e.g., herbivores) increase in sheltered zones. This pattern is marked in Labridae (particularly the genus *Halichoeres)*, Scaridae (*Scarus* sp.) and Pomacentridae (*Stegastes* sp.). Similar to what was found in some southern Caribbean reefs such as in Venezuela (Rodríguez and Villamizar 2000), the scarid *Scarus iseri* and the pomacentrid *Stegastes planifrons* are two of the most common fishes particularly in sheltered zones in Bocas del Toro, feeding on green turf algae that grows between branches or the coral *Porites* spp. and *Agaricia* spp. However, with the exception of *S. iseri*, none of the dominant species in Bocas del Toro are also dominant further North in Honduras (Clifton and Clifton 1998).
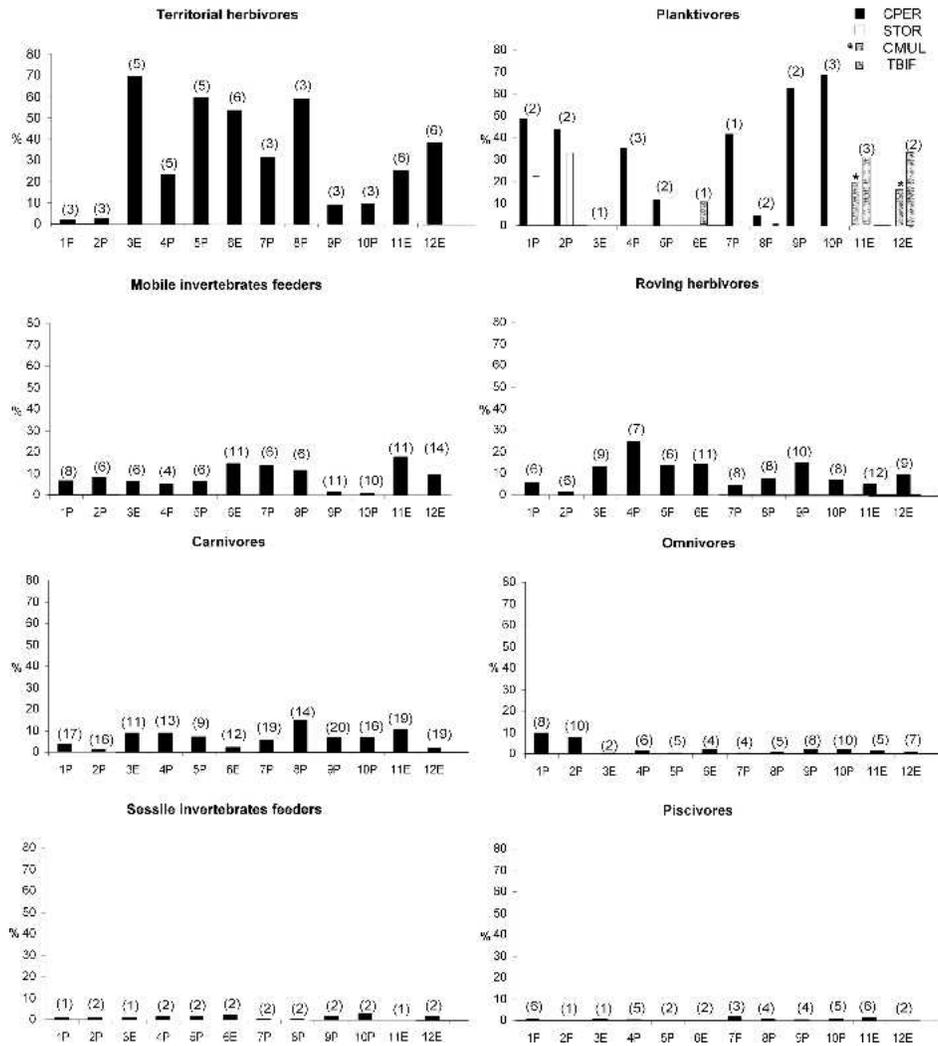
FIG. 9. Frequency, in percent, of the principal trophic groups in the different study zones; numbers in parenthesis indicate the number of species in each group. E = Exposed zone; P = Protected zone.

The species associations at exposed complex rocky shores and fire-coral reefs in Bocas del Toro (right side the CCA diagram) were similar to those of exposed coral reefs in Puerto Rico, but here there are no reported records of invertebrate feeders such as *Halichoeres poeyi* (HPOE) and *Halichoeres maculipinna* (HMAC) at exposed zones and in the same study an association between *Hypoplectrus chlorurus* (hamlets), *Stegastes planifrons* (SPLA), and *Holocentrus rufus* in areas of low water movements were found (McGeehee 1994). In Bocas del Toro, this association is replaced with similar genera but different species of hamlets along with schools of roving herbivores that can overcome the aggressiveness of damselfishes (Robertson et al. 1976). Haemulids were also present, and they may migrate from adjacent areas of mangroves. And the genus *Serranus* spp and *Coryphopterus dicrus* (CDIC) are typical inhabitants of sand-rubble areas. According to Floeter et al (2004), some of the species that were not associated to any particular habitat in our study are considered highly mobile and relatively sedentary *(Sparisoma* spp. and *Chaetodon capistratus* respectively). Even

Stegastes partitus is considered as territorial herbivore was in most zones. We believe that this is due to the fact that *S. partitus* is an omnivore that can either feed on zooplankton, small invertebrates and/or benthic algae at different exposed or sheltered zones (Booth and Hixon 1999). Differences in feeding behaviour among species of the same genus are an important factor in defining distributional patterns in Bocas del Toro as well. Randall (1967) found that the two species of blennies *Ophioblennius atlanticus* and *Parablennius marmoreus* have different feeding behaviour; the former feeding on algae growing in rocky shores and the latter, besides feeding on algae, feeds on many soft substrate animals that can often be found on patchy sandy habitats. The same author also found that *Halichoeres bivittatus* shows a higher feeding plasticity compared to other species on the genus and this is indicated by the many prey items found in their stomachs. This may be the reason why it is widely distributed on the different exposed and protected zones in Bocas del Toro. The more specialized foragers of the genus such as *Halichoeres radiatus* and *H. maculipinna* are present in the more complex exposed zones were they feed on particular food resources.

The species richness in Bocas del Toro is intermediate when compared with other studies from the Caribbean (Florida Keys 74 spp. McKenna 1997; Puerto Rico 71 spp. McGhee 1994; South-eastern Brazil 91 spp. Ferreira et al. 2001; Gulf of México 153 spp. Pattengill et al. 1997; Honduras 214 spp. Clifton and Clifton 1998; Colombia 273 spp. Mejía et al. 1998) and similar to that along the Pacific coast of the Isthmus (Gulf of Chiriquí, Dominici-Arosemena and Wolff unpublished data). Many of the regions of similar or lower species richness seem to lie close to the mainland and being affected by the runoff of rivers and environmental seasonality (Venezuela 68 spp. Rodríguez and Villamizar 2000; Costa Rica 48 spp. Sierra and García 1996). This situation also holds for Bocas del Toro.

Besides the consequences of geological changes (Coates et al. 1992), reef structure is regarded as a direct consequence of wave energy, while coral community structure, and to a greater extent fish community structure, seems a complex, indirect and non-linear consequence of reef structure and environmental conditions (Bradbury and Young 1981). In some studies, no correlation was found between fish diversity and habitat complexity (Ault and Johnson 1998; Clarke 1988). Studies in the Red Sea also suggest that coral cover has little influence on the species richness and abundance of fish (Roberts and Ormond 1987; Luckhurst and Luckhurst 1978). These findings are confirmed in Bocas de Toro due to the high abundance of small serranids and gobids in little complex rubble sand areas. We did, however, find positive correlations of species richness with hard substrates (massive corals and rocky complex reefs) along with an inverse correlation with monotony (less diverse substrate). It is suggested that the diverse strata in Bocas del Toro provide more niches and shelter, and thus increase species richness. Coral cover is also important in enhancing the physiographic structure in many of the more complex sheltered coral reefs in Bocas del Toro (e.g., zones 9 and 10). Recent studies on the Red Sea, by Khalaf and Kochzius (2002) also found total fish abundance and species richness to positively correlate with hard substrate and habitat diversity.

Waves and tides may play an important role in modifying the habitat structure (and by this increasing complexity) due to shaping of rocks and morphology of corals (Bradbury and Young 1981). In Bocas del Toro, exposed zones are physically more complex and the fish community is more diverse. But besides the influence of exposure in shaping the habitat, the presence of diverse and abundant food resources (e.g., oceanic plankton) is notorious in these exposed zones. Under these conditions, also sessile invertebrates (e.g., sponges) and algae increase the substrate diversity and allow, along with the rich food supply, for the occurrence of additional fish species.

The variability in reef fish larval transport and settlement is determined by the interaction of water masses and the effects of external forcing such as winds and tides.

In areas of low tidal variation, such as Bocas del Toro, winds may play an important intermittent role in larvae input to inshore sheltered zones while currents may play an important role for settlement and recruitment in exposed zones (Cowen 2002). Many horizontal patterns of community structure were described with respect to shore proximity, including occasional, completely isolated embayment (or lagoonal) assemblages. While water physics is important, larval distribution is not merely the result of passive dispersion by currents and tides. Particularly in areas of low current flow and small tidal range, many studies have found a high concentration of pomacentrid/gobiid larvae (see review by Cowen 2002). There is no information of larvae assemblages in Bocas del Toro, but our results indicate that these aforementioned families are the most abundant post-recruits in sheltered zones. From a comparative Mesoamerican perspective, patterns of spatial variation could markedly differ between Tropical Eastern Pacific (TEP) and Tropical Western Atlantic (TWA), since different oceanographic conditions could lead to differences in spatial patterns diversity. The large tidal fluctuation observed in the TEP (which can be several meters) in comparison with TWA (0.5 m) may facilitate larval transportation, settlement, and recruitment across a wider range of habitats than in the TEP.

Another reason for the spatial difference in the number of genera and species of reef fish in the study area may be the "habitat patchiness effect". Recent studies have found that the degree and the scale of habitat patchiness may be associated with fish diversity. Acosta and Robertson (2002) emphasize that species assemblages of small isolated habitat patches will constitute only a subset of the assemblage of a large patch reef, and the patterns of reef fish diversity may thus be highly scale dependent. In our study area the community differences were clearly marked between exposed and sheltered zones, although the total area per zone included in our sampling units were of the same size (600 m^2 in each habitat). We suggest that, with the exception of the continuous rocky reef (zones 11 and 12)

and fire coral fringing reef (zone 6) areas, most of the sheltered zones can be considered as relatively isolated discontinuous patches, separated mostly by sand, sea grass and mangroves (Guzmán and Guevara 1998b). Even if we pool all these zones and count the total number of species, it will be lower than that of massive corals and exposed rocky and fire coral reef ones. This suggests that these types of habitat are vitally important for the fish species richness in Bocas de Toro due to their complexity, level of exposure, and interconnectivity with other substrates. It is also important to mention that in the province of Bocas del Toro we can find a particular "nestedness" of select families of obligated reef fishes in sheltered zones (e.g., aggregation of gobiids and pomacentrids). These nesting patterns seem to be associated with recruitment limitation at the reef scale (McLain and Pratt 1999).

Particular mobility guilds were found in Bocas del Toro, which were specific to certain zones: better swimmers are adapted to exposed rocky zones of strong currents. Small site attached species and territorial herbivores are present in high numbers in sheltered zones of massive and foliaceous coral reefs with little current influence. Most studies regarding these mobility guilds focused only on labrids and tried to link their swimming performance to fin morphology (Bellwood and Wainwright 2001; Bellwood et al. 2002). There is still no knowledge about the swimming ability of many of the other reef fish, however, and questions regarding their ability for vertical and horizontal movements after settlement and recruitment on different types of reef can as yet not be answered. We found a marked difference in the presence/absence of species (within families) between exposed and sheltered zones in Bocas de Toro. Besides labrids, spatial differences were found in species of territorial herbivores and scarids. While improved swimming performance is definitely an advantage in exposed zones with higher structural complexity and shelter availability, there must be a trade of between the energy loss for this high swimming activity and the energy gain through the high food

abundance. Further research needs to determine if the distribution of certain species is more related to their swimming performance or/and type of food.

It seems that in the northern part of the Caribbean such as in the Gulf of México (including the Florida Keys), planktivores and invertebrate feeders dominate, while herbivores are low in numbers compared to Bocas del Toro (Bohnsack and Bannerot 1986; Pattengil et al. 1997). Here territorial herbivorous fishes are abundant and the areas they defend can cover over 80% of the surface of some reef habitats (Robertson and Lassig 1980; Ferreira et al. 1998; Ceccarelli et al. 2001). Ferreira et. al. (1998) mentioned that this trophic group may greatly depend on the physical structure of the coral reef and the distribution of the associated benthic organisms. An important part of the diet of some herbivores (e.g., *Scarus iseri*) is detritus and/or calcified material (Randall 1967). Browsing scarids (e.g., *Sparisoma*) that feed on some types of macro algae increase in abundance along with this food source at exposed and heterogeneous complex zones. Roving herbivores such as acanthurids have preference for certain types of algae common in exposed reef flats (Sluka and Miller 2001). Planktivores (e.g., *Serranus tortugarum*) at sheltered areas account for 20 to 70% of fishes in certain zones of rubble-sand. They swim above the bottom to mainly feed on demersal plankton (e.g., amphipods and harpadicoids copepods), found in low current areas (Randall 1967; Morales, Alvaro pers. comm.). This type of habitat is similar to that proposed by Parrish and Boland (2004) who called it "banks with infrequent relief features", where planktivorous are most numerous and benthic carnivores increased with an increased substrate complexity.

Bocas del Toro has been subjected to anthropogenic disturbances in recent years, due to its increasing importance as a popular tourist destination in the Republic of Panama. This will increase the human activities such as artisanal extractions, sport fishing and the use of the environmental landscape due to diving activities. This region lacks previous baseline data that could be used to organize sustainable fishery practices for the region. This study has provided the first description of the reef fish community structure, which can be used to help define areas of protection (Sale 2002). Even though more relevant studies are required to evaluate these ideas, we suggest that Bocas del Toro is an isolated site, where the population are likely to be maintained by self-recruitment and this types of regions needs particular guidelines to establish management plans (Sponaugle et al. 2002). Most of the smallest post recruit and juveniles that we found in our transects in sheltered zones belong to species that may have shorter pelagic larval duration (e.g., Gobiidae, Pomacentridae, Serranidae) in comparison to muraenids, balistids and tetraodontids that are families with the longest larval duration of reef fish families and were present occasionally only in exposed zones or in very lower numbers if not virtually absent in sheltered zones (Floeter and Gasparini 2000; Leis and McCormick 2002; Robertson 2001). In addition, in closed, shallow regions such as the internal sheltered zones of Bocas del Toro with low water circulation and changes in surface salinity may negatively affect the species richness of the Ichthyoplankton (Dominici-Arosemena et al. 2000; Romero 1992). Despite a few interconnected coral reefs in Southern Costa Rica, much of the remaining coastline stretching to the Southern boarder of Nicaragua is unsuitable for reef development due to sandy substrate, coastal marshes in the North, and the input of freshwater by San Juan River (Cortés pers. comm.). The abundance of larvae being transported from the reefs in Southern Nicaragua southwards are likely to decline resulting in low recruitment in Bocas del Toro. Thus, the distance from Northern reef develop areas and the presence of suitable interconnected substrate for larval settlement in neighbouring regions, may constitute an important function of settlement and recruitment in Bocas del Toro. We suggest that as a result of its particular oceanographic regime, larval recruitment may be low in Bocas del Toro and even what would normally be considered an average fishing pressure may be unsustainable. The

highest-populated centres of the Bocas region are located at Isla Bastimentos, Isla Colón, and Carenero island, where some of the massive coral and rocky reefs are located. In our study we confirm that rocky zones are rich in species and should be included within the limits of the Bastimentos National Park (e.g., rocky shores of Bastimentos Island and areas of spear or other artisanal fisheries). In other studies, the reduction of three-dimensional structure has been identified as one cause for the shift in species composition (McKenna 1997), a process that is currently underway due to physical destruction of habitat (e.g., reef fishing, anchoring); which will directly or indirectly affect the fish community structure. Our results indicate a negative correlation of fish diversity with either the percentage of dead coral substrates and/or low substrate diversity zones (rubble, dead corals live branching and foliaceous corals) that normally result from habitat destruction or the growing of opportunistic species of corals due to the high sediment deposition (Cortés 1984). Our study supports the need for: 1. the protection of many reef areas and their benthic fauna (especially those zones of massive and fire coral cover) (for delineation of these areas, see Guzmán and Guevara 1998a,b, 1999); 2. the education of tourists to not destroy or extract the benthic flora and fauna; and 3. restrict the fishing activities in coral reef areas. There is also a need to delimit all reef zones to avoid anchorage of boats in reef areas. In addition, other anthropogenic impacts (e.g., sediment deposition from extensive banana plantations) are also affecting this area. For these regions, habitat degradation of the benthic fauna and flora could be faster than expected. The present situation of Bocas del Toro may already represent a fish community structure subject to human induced changes.

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APPENDIX. List of species found and their distribution in the study zones (1-12). TL = Trophic Level; C = Carnivorous; I = mobile Invertebrates; O = Omnivore; P = Piscivore; PL = Planctivore; RH = Roving Herbivore; SI = Sessile Invertebrate feeder; TH = Territorial Herbivore.

Family/Name	TL	1	2	3	4	5	6	7	8	9	10	11	12
ACANTHURIDAE													
Acanthurus bahianus	RH	X	X	X	X	X	X	X	X	X	X	X	X
Acanthurus chirurgus	RH	X	X	X	X	X	X			X	X	X	X
Acanthurus coeruleus	RH	X		X	X	X	X	X		X	X	X	X
APOGONIDAE													
Apogon townsendi	MI										X		
Apogon pseudomaculatus	MI											X	
AULOSTOMIDAE													
Aulostomus maculatus	C			X			X	X	X	X	X		
BALISTIDAE													
Aluterus scriptus	O											X	
Balistes vetula	SI											X	
Cantherhines pullus	O											X	X
BLENNIDAE													
Ophioblennius atlanticus	TH						X					X	X
Parablennius marmoreus	O	X	X					X		X	X		
BOTHIDAE													
Bothus lunnatus	C												X
CARANGIDAE													
Carangoides bartholomaei	P	X								X	X	X	
Caranx crysos	P			X	X		X	X	X	X	X	X	X
Caranx ruber	P	X	X	X	X		X	X	X	X	X	X	X
Chloroscombrus chrysurus	Pl										X		
Decapterus punctatus	C				X				X	X	X		
Decapterus sp.	C				X			X					
CHAETODOTIDAE													
Chaetodon capistratus	SI	X	X	X	X	X	X	X	X	X	X		X
Chaetodon ocellatus	O	X	X		X		X	X	X	X	X		X
Chaetodon striatus	SI		X		X	X	X	X	X	X	X		X
CIRRHITIDAE													
Amblycirrhitus pinos	C											X	
DASYATIDAE													
Dasyatis americana	O	X	X							X	X	X	
DIODONTIDAE													
Diodon holocanthus	MI									X			
Diodon hystrix	MI										X		X
ELOPIDAE													
Megalops atlanticus	C								X				
GERREIDAE													
Gerres cinereus	MI	X	X								X		
GINGLYMOSTOMATIDAE	MI												
Ginglymostoma cirratum	C	X	X										
GOBIIDAE													
Coryphopterus dicrus	O	X	X			X				X	X		
Coryphopterus personatus	PL	X	X		X	X		X	X	X	X		
Gnatholepis thompsoni	O										X		
Ctenogobius saepepallens	O	X	X										
Elacatinus dilepsis	O										X		
Elacatinus xanthiprora	O	X	X			X				X	X	X	
Elacatinus sp.	O		X										
GRAMMATIDAE													
Gramma loreto	MI											X	

APPENDIX. Continued.

Family/Name	TL	1	2	3	4	5	6	7	8	9	10	11	12
HAEMULIDAE													
Anisotremus surinamensis	C											X	
Anisotremus virginicus	MI	X			X		X	X		X	X	X	X
Haemulon aurolineatum	MI		X			X	X	X	X	X		X	X
Haemulon carbonarium	MI	X					X			X		X	
Haemulon chrysargyreum	MI						X	X					
Haemulon flavolineatum	MI			X	X	X	X	X	X	X	X	X	X
Haemulon macrostomum	MI			X		X	X				X	X	X
Haemulon parra	C									X			
Haemulon plumierii	C	X	X	X	X	X	X	X	X	X	X	X	X
Haemulon sciurus	C	X					X					X	X
HOLOCENTRIDAE													
Holocentrus adscensionis	C	X	X	X	X	X	X	X	X	X		X	X
Holocentrus rufus	C							X			X	X	X
Myripristis jacobus	C							X	X			X	X
Neoniphon marianus	MI								X				
Sargocentron vexillarium	C										X	X	X
KYPHOSIDAE													
Kyphosus sectator	RH						X		X			X	
LABRIDAE													
Bodianus rufus	MI											X	X
Halichoeres bivittatus	MI	X	X	X	X	X	X			X	X	X	X
Halichoeres garnoti	MI							X	X	X	X	X	X
Halichoeres maculipinna	MI	X		X			X					X	X
Halichoeres pictus	MI											X	X
Halichoeres poeyi	MI			X			X					X	X
Halichoeres radiatus	MI											X	X
Lachnolaimus maximus	MI									X			
Thalassoma bifasciatum	PL		X	X	X	X	X	X	X	X	X	X	X
LABRISOMIDAE													
Labrisomus nuchipinnis	C											X	
Malacoctenus triangulatus	MI		X				X				X	X	X
LUTJANIDAE													
Lutjanus analis	C	X	X				X	X		X	X	X	X
Lutjanus apodus	C	X	X				X		X	X	X	X	X
Lutjanus cyanopterus	C												X
Lutjanus griseus	C	X			X			X		X			
Lutjanus jocu	C	X	X					X					
Lutjanus mahogoni	C	X			X		X			X		X	
Lutjanus synagris	C		X									X	
Ocyurus chrysurus	C	X	X	X	X	X	X	X	X	X	X	X	X
MALACANTHIDAE													
Malacanthus plumieri	C		X										
MULLIDAE													
Mulloidichthys martinicus	MI	X	X			X	X	X		X	X	X	X
Pseudupeneus maculates	C	X	X	X	X	X		X	X	X	X	X	X
MURAENIDAE													
Echidna catenata	C												X
Gymnothorax miliaris	C												X
OPISTOGNATHIDAE													
Opistognathus aurifrons	PL	X	X	X			X					X	
OSTRACIIDAE													
Lactophrys triqueter	O												X

APPENDIX. Continued.

Family/Name	TL	1	2	3	4	5	6	7	8	9	10	11	12
PEMPHERIDAE													
Pempheris schomburgkii	PL						X					X	
POMACANTHIDAE													
Holacanthus ciliaris	O			X		X				X		X	X
Holacanthus tricolor	O		X						X		X		X
Pomacanthus arcuatus	O		X	X	X	X		X	X	X	X		
POMACENTRIDAE													
Abudefduf saxatilis	O			X	X	X			X		X		X
Chromis cyanea	PL											X	
Chromis multilineata	PL											X	X
Microspathodon chrysurus	TH		X	X	X	X						X	X
Stegastes adustus	TH		X	X	X	X						X	X
Stegastes leucostictus	TH	X	X	X	X	X	X	X	X	X	X	X	X
Stegastes partitus	TH	X	X	X	X	X	X	X	X	X	X	X	X
Stegastes planifrons	TH	X	X	X	X	X	X	X	X	X	X	X	X
SCARIDAE													
Scarus coelestinus	RH		X				X	X	X	X		X	
Scarus iseri	RH	X	X	X	X	X	X	X	X	X	X	X	X
Scarus taeniopterus	RH									X			
Scarus vetula	RH											X	
Sparisoma aurofrenatum	RH		X	X	X	X	X	X	X	X	X	X	X
Sparisoma chrysopterum	RH	X	X				X	X	X	X	X	X	X
Sparisoma radians	RH			X			X					X	X
Sparisoma rubripinne	RH			X	X		X	X	X	X	X	X	X
Sparisoma viride	RH	X	X	X	X	X	X	X	X	X	X	X	X
SCIAENIDAE													
Equetus punctatus	MI	X						X	X	X			
Odontoscion dentex	C			X				X	X	X	X	X	
SCOMBRIDAE													
Scomberomorus maculatus	P	X			X								
Scomberomorus regalis	P	X			X	X				X		X	
SERRANIDAE													
Epinephelus adscensionis	C									X	X		
Cephalopholis cruentata	C	X	X	X	X	X	X	X	X	X	X	X	X
Cephalopholis fulva	C									X		X	X
Epinephelus guttatus	C									X		X	X
Epinephelus striatus	C												X
Hypoplectrus aberrans	C							X					
Hypoplectrus guttavarius	C									X			
Hypoplectrus indigo	C		X					X					
Hypoplectrus nigricans	C	X	X	X	X	X		X	X	X	X		
Hypoplectrus puella	C	X	X	X	X	X	X	X	X	X	X		
Hypoplectrus sp.	C	X	X	X	X	X	X	X		X			
Hypoplectrus unicolor	C	X	X	X	X	X		X	X	X	X		
Mycteroperca venenosa	C										X		
Rypticus maculatus	C						X						
Rypticus saponaceus	C												X
Serranus baldwini	MI											X	
Serranus tigrinus	MI	X	X	X	X	X				X	X	X	X
Serranus tortugarum	PL	X	X		X								
SPARIDAE													
Archosargus rhomboidalis	O	X			X		X						
Calamus penna	MI	X	X			X				X			
SPHYRAENIDAE													
Sphyraena barracuda	P	X			X		X		X			X	

APPENDIX. Continued.

Family/Name	TL	1	2	3	4	5	6	7	8	9	10	11	12
SYNODONTIDAE													
Synodus intermedius	P	X						X		X	X	X	
TETRAODONTIDAE													
Canthigaster rostrata	O	X	X	X	X	X		X	X	X	X	X	X
Sphoeroides spengleri	O	X								X			
UROLOPHIDAE													
Urobatis jamaicensis	C	X											