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Journal of Experimental Marine Biology and Ecology 315 (2005) 31–47

**Journal of  
EXPERIMENTAL  
MARINE BIOLOGY  
AND ECOLOGY**

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## Biogeographic patterns of coastal fish assemblages in the West Indies

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Received 2 March 2004; received in revised form 24 August 2004; accepted 30 August 2004

### Abstract

This paper explores the factors influencing or controlling West Indies reef fish assemblages, using an extensive underwater survey (mensurative experiment). The sampling units represented variation in substrate type, depth, and geography. For that, the distribution of coastal species assemblages was examined in different islands, from the Dominican Republic in the north to Bequia (Grenadines) in the south. Visual surveys were made by snorkeling and SCUBA diving in various habitats from the surface to 55 m deep. Presence–absence data from 248 sites and 228 species were analysed by canonical redundancy analyses. Three quantitative variables (depth, latitude, and location of the sites along the Caribbean arch) as well as qualitative descriptors corresponding to 10 habitat types were used as explanatory variables in the canonical analyses. Variation partitioning showed that substrate was the most important factor, accounting for 15.2% of the species variation, while the geographic gradients explained 8.4%; 2.3% was explained jointly by the two groups of variables. Most of the variation explained by depth was also accounted for by the substrate categories. In a canonical analysis of community composition by substrate types, the first canonical axis divided the sites into soft substrates characterized by few species and hard substrates characterized by several other species. The second axis separated the outer reef slopes, with low or high coral cover and sandy areas with coral patches (deep habitats) from shallow non-reef rocky substrates and reef fronts. A second canonical analysis of community composition by geographic gradients produced an ordination of the sites in which the succession of islands along the Caribbean arch is recognizable. The species are positioned in the ordination according to their contributions to the fauna of the various islands. This paper supports the hypothesis that fish community composition in the Caribbean islands is controlled mostly by a latitudinal and a hydrologic gradient, as well as by the type of habitat and, with a lower influence, by depth.

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**Keywords:** Biogeography; Canonical redundancy analysis; Caribbean arch; Coral reefs; Coastal areas; Fish assemblages; Geographic gradients; Survey; West Indies

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## 1. Introduction

Many studies have shown that coral reef fish communities display a very heterogeneous spatial structure, which often reflects the diversity of habitats in the studied areas (Gladfelter and Gladfelter, 1978; Alevizon et al., 1985; Roberts and Ormond, 1987). Heterogeneity occurs at the local reef scale as well as on a regional scale. Williams (1991) synthesized knowledge concerning the distribution of reef fishes on coral reefs and pointed out the lack of data concerning Caribbean reef fishes. Up to now, published information on the geographic distribution of Caribbean fish species has only been available for the Bahamas (Alevizon et al., 1985), Cuba (Claro et al., 1990), the Virgin Islands (Gladfelter and Gladfelter, 1978), and the French West Indies (Bouchon-Navaro and Louis, 1986; Bouchon-Navaro, 1997; Bouchon-Navaro et al., 1997). Numerous descriptive studies on reef fish distributions are available for different Indo-Pacific reef areas (Indian Ocean: Harmelin-Vivien, 1977; Letourneur, 1996; Ohman et al., 1997; Red Sea: Edwards and Rosewell, 1981; Roberts and Ormond, 1987; and Pacific Ocean: Talbot and Goldman, 1972; Chave and Eckert, 1974; Williams, 1982; Galzin, 1987; Morize et al., 1990; Kulbicki, 1997). These studies generally concern small geographic areas; only a few authors have worked at broad scale (Talbot and Gilbert, 1981; Williams, 1982; Williams and Hatcher, 1983; Williams et al., 1986; Galzin, 1987; Hilomen and Gomez, 1988; Galzin et al., 1994; Letourneur et al., 1997).

The distribution of fish species on coral reefs has been related to several factors (e.g., substrate complexity, food availability, water quality, presence of current, wave exposure, available shelters, and coral cover: see Williams, 1991). In the present study, survey data collected in the West Indies from the Dominican Republic in the north to the Grenadines in the south of the Lesser Antilles are used to test the hypothesis that fish community composition in the Caribbean islands is controlled by latitudinal and hydrologic gradients, as well as by substrate type and depth. The survey (mensurative experiment sensu Hurlbert, 1984) represented variation in substrate type, depth, and geography.

## 2. Methods

### 2.1. Field methods

In the coastal zones of the different islands (Fig. 1), visual surveys were conducted in various habitats, from the surface to 55 m depth, by snorkeling in the shallowest areas and by SCUBA diving in deeper zones. A dive consisted of a survey from 30 to 40 min where the same observer (Y B-N) made a list of observed fish species. For Caribbean reef fish, a qualitative sampling of 30 min had been found to be sufficient to flatten the time-species curve (Bouchon-Navaro et al., 2000). The diver remained at the same depth and in the same type of habitat during each visual survey. The area covered by each qualitative survey was approximately 1000 m<sup>2</sup>. Because all sites were surveyed by the same observer (Y B-N), the data were comparable and could be used in the analyses, although they may be subject to the observer's bias. The surveys were conducted as part of environmental assessment work carried out in various islands of the Caribbean crescent for 13 years (1982 to 1995). There was no temporal pattern in the sampling design. A total of 248 sites were surveyed in the West Indies. The sites were distributed from north to south as follows: 10 in Puerto Viejo (PV) in the Dominican Republic, 26 in Anguilla (AN), 43 in Saint Martin (SM), 32 in Saint-Barthélemy (SB); 64 sites in the Guadeloupe archipelago (GU), located in four areas: Grand Cul-de-Sac Marin (CS), Pigeon Island (PG), Saint-François (SF), and Marie-Galante (MG); 50 sites in Martinique (MA), and 23 in Bequia (BQ) in the Grenadines. The exact locations of the sites are given in Bouchon-Navaro (1997). Table 1 summarizes the distribution of the 248 survey sites according to the types of habitat and depth classes in the seven islands.

### 2.2. Statistical analyses

The 'sites by species' community composition table (248×231) contained presence-absence data. They were subjected to the Hellinger transformation, which consists in expressing each presence as a fraction of the total number of species observed at the site and taking the square root of the fraction. Legendre and Gallagher (2001) have shown that this



Fig. 1. Surveyed sites (bold names) in the Caribbean.

transformation makes species presence-absence or abundance data amenable to linear ordination methods such as principal component analysis (PCA) or canonical redundancy analysis (RDA).

The following explanatory variables were used in the analyses: (1) 10 habitat types (binary variables): SA: pure sand areas; SC: sandy areas with coral patches; SG: seagrass beds; BC: seagrass beds with coral patches; FN: fields of coralline nodules; RF: reef flats; RC: reef fronts; OLC: outer reef slopes with low coral cover; OHC: outer reef slopes with high coral cover; RS: non-reef rocky substrates (Table 1). (2)

Geographic gradients: latitude and location of the sites along the Caribbean Arch. Latitude was included to test the hypothesis that community composition varied along the latitudinal gradient: the site latitude values ranged from  $13^{\circ}$  to  $18^{\circ}30'N$ . Position along the Caribbean arch tested the hypothesis of an influence of the northward current that dominates the hydrology of the Antilles, which is a combination of the North-Equatorial and Guiana currents. Bequia (BQ) had position 0. The islands received increasing position values along a broken line going from island to island, in the following order: Bequia (BQ), Martinique

Table 1  
Number of survey sites (total: 248) by habitat class (top) or depth class (bottom) in each island

	PV	AN	SM	SB	GU	MA	BQ	No. of survey sites
<i>Habitat classes</i>								
SA: pure sand areas	1	0	0	0	3	2	1	7
SC: sandy areas with coral patches	0	0	0	1	2	11	2	16
SG: seagrass beds	0	9	0	4	4	1	5	23
BC: seagrass beds with coral patches	3	4	0	2	1	2	1	13
FN: fields of coralline nodules	0	0	0	2	0	0	6	8
RF: reef flats	2	3	0	1	12	0	3	21
RC: reef fronts	3	0	5	0	7	3	0	18
RS: rocky substrates	0	10	3	7	7	6	2	35
OLC: outer slopes, low coral cover	0	6	3	6	1	3	0	19
OHC: outer slopes, high coral cover	1	11	15	9	27	22	3	88
<i>Depth classes</i>								
1–10 m	10	13	34	18	40	26	17	158
11–20 m	0	13	9	12	18	21	4	77
21–30 m	0	0	0	2	2	3	2	9
31–40 m	0	0	0	0	3	0	0	3
55 m	0	0	0	0	1	0	0	1

Island codes: PV=Puerto Viejo (in the Dominican Republic), AN=Anguilla, SM=Saint Martin, SB=Saint-Barthélemy, GU=Guadeloupe (GU), BQ=Bequia (in the Grenadines).

(MA), Guadeloupe (GU; sites CS, MG, PG, SF all received the same island position), Saint-Barthélemy (SB), Saint Martin (SM), Anguilla (AN), and Puerto Viejo (PV) in the Dominican Republic. Latitude and position along the Caribbean arch were centred on their respective means and developed (separately) as third-order polynomials, in order to allow the expression of nonlinear effects of these variables on community composition. (3) Water depth (quantitative variable: 1 to 55 m, coded in five depth classes).

Variation partitioning (Borcard et al., 1992; Borcard and Legendre, 1994) was computed to partition the variation of the Hellinger-transformed fish community composition data among three or four groups of explanatory variables: substrate classes, geographic gradients (latitude and Caribbean arch), and depth. Partitioning among three explanatory matrices has been described by Quinghong and Bråkenhielm (1995) and Anderson and Gribble (1998). Canonical partitioning and tests of the fractions of variation were performed using a program written by P. Legendre.

The transformed fish data were related to the explanatory variables using the RDA procedure of the program CANOCO version 4.5 (ter Braak and

Smilauer, 2002). In this method, the ordination axes are constrained to be linear combinations of the environmental variables (Rao, 1964; Legendre and Legendre, 1998). Permutation tests provided information on the statistical significance of the species–environment canonical relationship.

### 3. Results

A total of 228 identified species, plus 3 unidentified juvenile species, belonging to 59 families were observed during the present study (Appendix A). Table 2 gives the number of families and species observed at the survey sites in the seven islands. Search for a trend in these numbers was conducted by computing Kendall's rank correlation coefficients between the four fish variables in Table 2 and the rank order of the islands (Kendall and Ord, 1990). A significant Kendall's coefficient, at the 5% significance level, was only found for the number of species per survey in reef areas ( $P=0.002$ ). That suggests the existence of a decrease in fish biodiversity per unit of reef surface along the Caribbean arch from Bequia to Puerto Viejo in the Dominican Republic.

Table 2

Island coordinates, number of fish families and species per survey, and number of species in all habitats and in the reef areas only

Islands	Latitude °N	Longitude °W	No. of families	No. of species	Average number of species per survey in	
					All habitats	Reef areas
Puerto Viejo (Dominican Republic)	18.3	70.5	28	63	18	22
Anguilla	18.2	63.1	39	113	26	26
Saint Martin	18.1	63.0	42	135	25	29
Saint-Barthélemy	17.9	62.9	34	114	26	30
Guadeloupe	16.3	61.6	48	167	30	32
Martinique	14.7	61.0	42	150	31	32
Bequia	13.0	61.2	45	123	24	33

The islands are presented in order of decreasing latitudes.

3.1. Variation partitioning

Fig. 2a shows the results of variation partitioning. Separately, the three main factors each explained a

significant portion of the variation of community composition ( $P=0.001$  after 999 permutations of residuals under the reduced model). Substrate classes were the main factor affecting variation. Two-thirds of

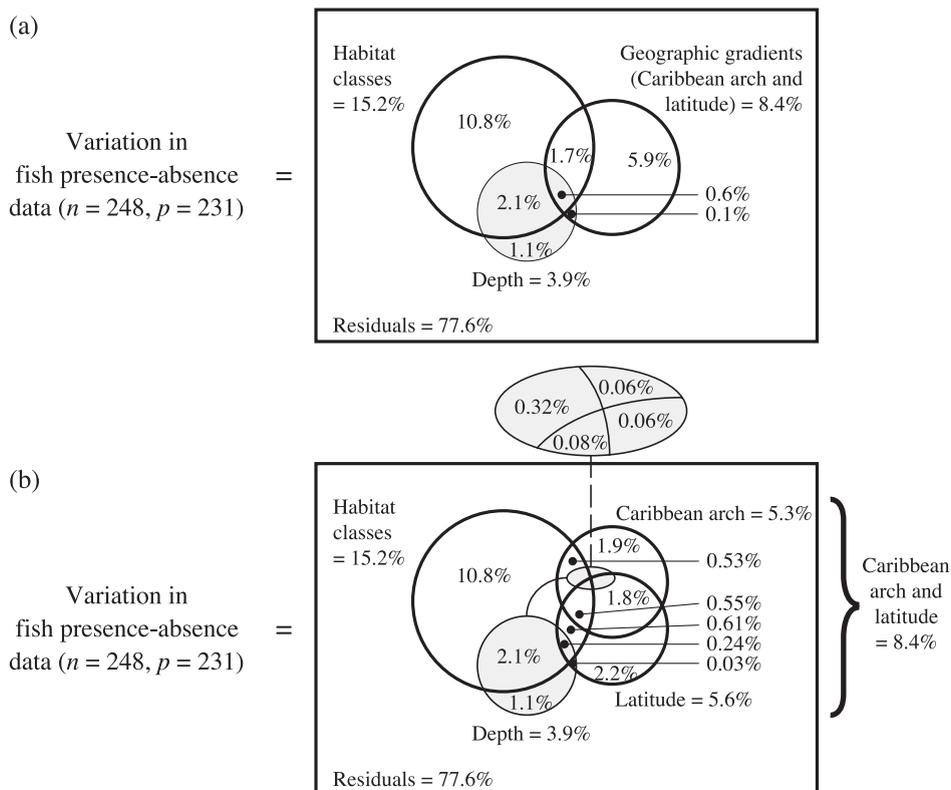


Fig. 2. (a) Variation partitioning results, given as percentage (%) of the variation of the Hellinger-transformed fish presence-absence data table, among three sets of explanatory variables (substrate classes, geographic gradients, and depth); (b) results of a refined analysis in which position along the Caribbean arch and latitude, each represented by a third-order polynomial, formed separate explanatory datasets. Since it is not possible to display four intersecting circles in a plane, the variation explained by depth is separated into a circle and an ellipse (grey). The contents of the ellipse are detailed above the graph. The proportions of variation depicted by the circles and ellipses are approximative.

the variation explained by depth was also explained by the substrate types. Three-quarters of the variation explained by the six geographic gradient variables were not explained by the substrate classes. The variation among islands is thus mostly independent of substrate classes, most substrate types being found in most islands. Some substrate types were, however, found mostly in the sites surveyed in some islands, causing the appearance of a significant fraction of variation (1.7%+0.6%=2.3%) explained jointly by the two sets of variables. This result was confirmed by analysing a contingency table crossing the islands to the substrate types (Table 1). This analysis showed that there are significant differences among islands in the distribution of substrate types ( $\chi^2=180.47$ ,  $df=54$ ,  $P<0.0001$ ). The fish community variation (8.4%), explained by the six geographic gradient variables, was identical to that explained by six dummy variables representing the seven islands. This result was expected because six correctly coded variables are sufficient to explain the variation among seven islands. A large amount of variation (77.6%) was not explained by the environmental and spatial variables. This was expected due to the large number of species present in the Caribbean Sea and the random appearance (and thus irregular recording) of species during a 30-min survey.

Fig. 2b shows the results of the partitioning with the three polynomial terms describing the positions of the islands along the Caribbean arch separate from the three polynomial terms describing latitude. In each case (arch and latitude), the 1st, 2nd, and 3rd degree polynomial terms were significant in a forward selection procedure of explanatory variables, showing that the relationship of community composition to arch position on the one hand, and latitude on the other hand, was not linear. Significance of these polynomial terms supported our two hypotheses of relationship of community structure to geography. The two geographic variables explained nearly the same proportion of the fish community variation (5.3% for position along the Caribbean arch, 5.6% for latitude), with about half of that proportion (2.5%) explained jointly by the two gradient polynomials. The amount of variation explained jointly by the geographic position variables and depth is small, totaling 0.8%.

These results indicate that we should analyse the community variation explained by substrate types and

then by geographic positions. Depth provides very little exclusive explanation (1.1%) besides the 2.1% that can also be explained by substrate types.

### 3.2. Species–substrate relationships

Canonical redundancy analysis showed that the 10 habitat classes explained 15.2% of the variation in the Hellinger-transformed species presence-absence data, as we saw in Section 3.1. The relationship was highly significant ( $P=0.001$  after 999 random permutations of residuals under the reduced model).

Fig. 3 is a biplot showing the species (lines) and habitat classes (squares) with respect to canonical axes 1 and 2. The 248 individual survey sites are not shown. The first two canonical axes explain 10.3% of the variation in the species data and 67.4% of the species–environment relationship. Only the 34 species that have a higher than 10% fit in the space of axes 1 and 2 are shown; those species are fitted at 14–50% in the full canonical space (nine axes). A few species are pointing to the right of the biplot, where soft bottom habitats are found; the most important ones in that group are: *Halichoeres poeyi* (Hal poe), *Sparisoma radians* (Spa rad), and *Halichoeres bivittatus* (Hal biv). The hard substrate habitats are found on the left of the figure. Most of the species vectors are pointing in that direction. The species that are best-fitted by the canonical plane and are pointing in the upper-left direction, towards the “outer reef slopes” with “low [or high] coral cover” and “sand with coral patches” substrates, are: *Halichoeres garnoti* (Hal gar), *Stegastes partitus* (Ste par), *Chromis cyanea* (Chr cya), *Cephalopholis fulva* (Cep ful), and *Holacanthus tricolor* (Hol tri). The most important species pointing in the lower-left direction, towards “non-reef rocky substrate” and “reef front”, are: *Sparisoma viride* (Spa vir), *Acanthurus coeruleus* (Aca coe), *Microspathodon chrysurus* (Mic chr), *Sparisoma rubripinne* (Spa rub), *Stegastes leucosticus* (Ste leu), *Abudefduf saxatilis* (Abu sax), *Ophioblennius atlanticus* (Oph atl), and *Halichoeres radiatus* (Hal rad).

The seven islands as well as the four Guadeloupe survey areas were projected as supplementary variables onto this biplot (triangles). They were not included in the canonical analysis. Their presence in Fig. 3 serves as a visual interpretation of the unbalance of the survey described in Table 1 (top).

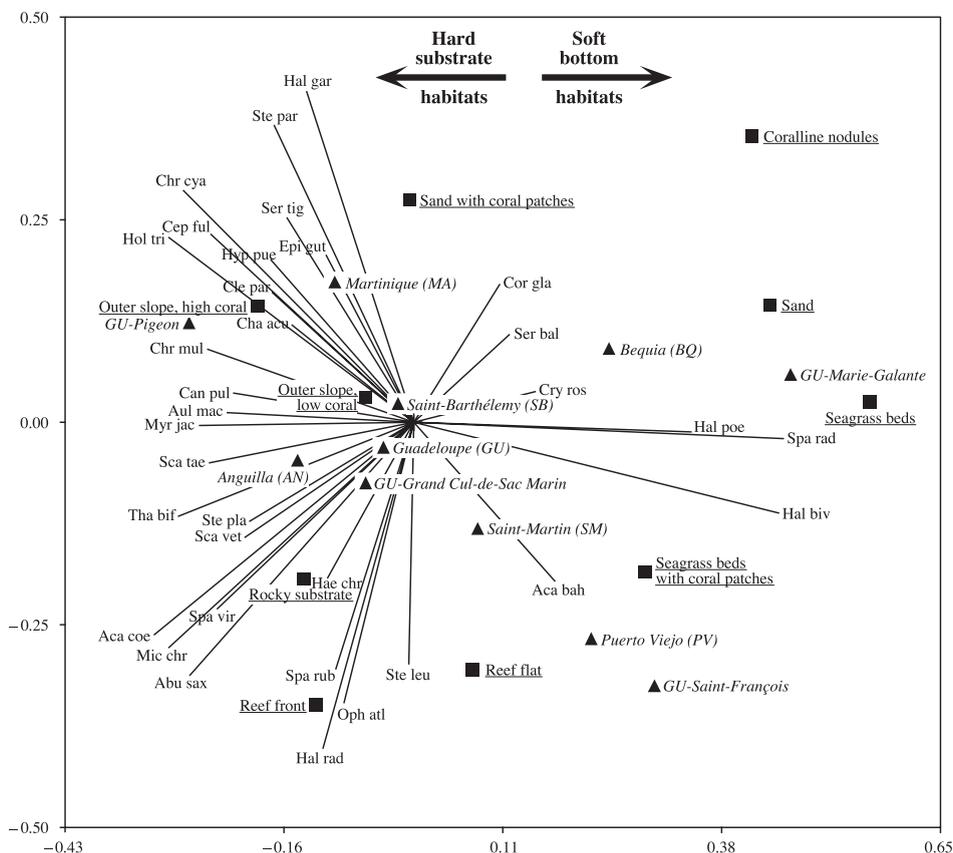


Fig. 3. RDA of fish presence-absence with respect to substrate types (squares). The centroids of the seven islands and the four Guadeloupe survey areas (triangles) are projected as supplementary variables. Lines: 34 species fitted at more than 10% in the space of canonical axes 1 and 2; the species coordinates were divided by 10. Proportion of the fish community composition variation accounted for by all nine canonical axes: 15.2%. Axis 1: 6.2%; axis 2: 4.1%.

For instance, many sites in Martinique (MA) were described as “sand with coral patches” and “outer slope, high coral cover”. The triangle representing Martinique is at the centroid of the positions of the individual Martinique sampling sites (not shown in the figure). It is near the symbols representing these two categories of environment. Many sites in Anguilla (AN) were classified as “seagrass beds”, “non-reef rocky substrates”, and “outer slope with high coral cover”; the triangle representing the centroid of the Anguilla survey sites is located in-between the symbols representing these three environmental categories in the graph. The four areas studied in Guadeloupe (GU) are quite varied in habitat composition.

### 3.3. Broad-scale biogeographic structure

Redundancy analysis was also used to study the biogeographic relationship of the Hellinger-transformed fish presence-absence data to the geographic gradients. The gradients explained 8.4% of the variation in the fish data, as we saw in Section 3.1; the relationship was highly significant ( $P=0.001$  after 999 random permutations of residuals under the reduced model).

Analysis of the community composition data by a table of dummy variables representing the seven islands produced the exact same canonical analysis as described above, with the same total amount of explained variation and the same canonical axes. It is

thus legitimate to represent the seven islands in Fig. 4; symbols for islands are located at the centroids of the sites surveyed in each island. The four Guadeloupe areas are represented by symbols located at the centroid of the corresponding survey sites.

The biplot in Fig. 4 shows the species (lines) and the six gradient variables (arrows) with respect to canonical axes 1 and 2; the 248 individual survey sites are not shown. The first two canonical axes explain 5.1% of the variation in the species data and 60.2% of the species–environment relationship. The quadratic and cubic gradient variables derived from latitude and position along the Caribbean arch, which were all statistically significant, indicate that community com-

position varied in a nonlinear fashion along these complementary gradients.

Only the 18 species that have a higher than 10% fit in the space of axes 1 and 2 are shown; those species are fitted at 11–46% in the full canonical space (6 axes). As shown in Table 2, the number of fish species per census generally decreases along the gradient from Bequia to Puerto Viejo, especially on the reefs. Most of the species shown in the figure are found in the right-hand portion of the graph. Three are ubiquitous species, found in all islands and in most or all sites of Guadeloupe: *Mulloidichthys martinicus* (Mul mar), *Chromis multilineata* (Chr mul), and *Stegastes partitus* (Ste par). Four species are found

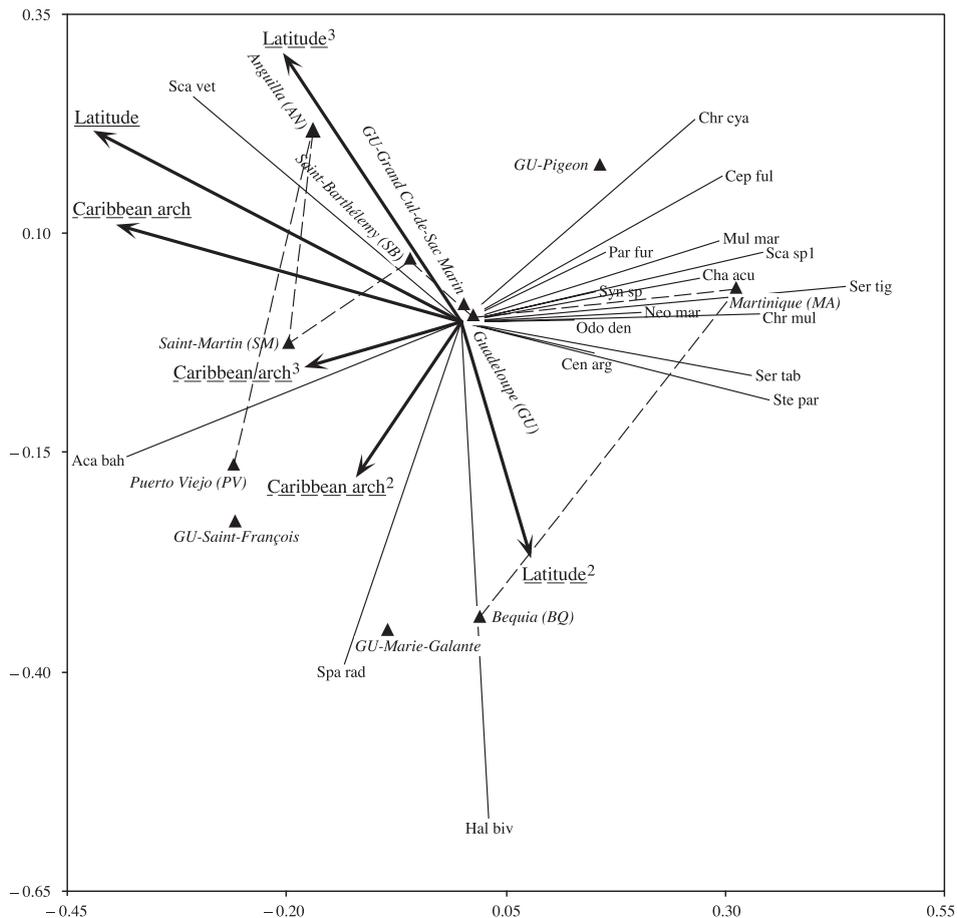


Fig. 4. RDA of fish presence-absence with respect to geographic gradients (bold arrows). The centroids of the seven islands and the four Guadeloupe survey areas (triangles) are projected as supplementary variables. The succession of islands along the Caribbean arch is materialized by a dashed broken line. Lines: 18 species fitted at more than 10% in the space of canonical axes 1 and 2; the species coordinates were divided by 10. Proportion of the fish community composition variation accounted for by all six canonical axes: 8.4%. Axis 1: 3.3%; axis 2: 1.8%.

in most or all islands, but not in the Saint-François area of Guadeloupe, hence the position of the Saint-François centroid in the third quadrant of the figure: *Chromis cyanea* (Chr cya), *Cephalopholis fulva* (Cep ful), *Serranus tigrinus* (Ser tig), and *Serranus tabacarius* (Ser tab). Three species were found in Bequia, Martinique and Guadeloupe (although not in Saint-François): *Paranthias furcifer* (Par fur), *Chaetodon aculeatus* (Cha acu), and *Neoniphon marianus* (Neo mar). Two species were found in Bequia and Martinique only: *Odontoscion dentex* (Odo den) and *Centropyge argi* (Cen arg), and two in Martinique only: *Scarus* sp.1 (Sca sp1) and *Synodus* sp. (Syn sp).

A few species are pointing to the left of the biplot; they are ubiquitous species. *Scarus vetula* (Sca vet) was found everywhere except in Martinique. *Acanthurus bahianus* (Aca bah) was seen in all sites, although less frequently in Martinique and in the Grand Cul-de-Sac Marin of Guadeloupe, hence its position in the third quadrant of the figure. *Sparisoma radians* (Spa rad) and *Halichoeres bivittatus* (Hal biv) were found in all islands except Anguilla; this is why these species' vectors are pointing downwards.

#### 4. Discussion

Robins (1971) estimated from 2000 to 2500 the number of fish species in the Tropical West Atlantic, half of them living in the coastal waters of continental shelves. Within the Caribbean area, 912 species are known from Cuban waters (Claro, 1994), between 500 and 600 in the Bahamas (Bölkhe and Chaplin, 1968) and Florida (Starck, 1968), and about 400 in the Virgin Islands (Clavijo et al., 1980). For comparison, about 800 coastal species, including reef and shore fishes, indigenous freshwater and epipelagic fishes, are known in Polynesia (Randall, 1985), and more than 1000 in New Caledonia (Rivaton et al., 1989). The relative paucity of the Caribbean ichthyofauna compared to the Indo-Pacific region (about 4000 species, see Myers, 1991) is well known. Species living in mangroves, pelagic species, as well as fish living in deep waters were not included in the present study. Destructive sampling techniques are necessary to collect species rarely observed by divers during the day, such as fishes living in the reef crevices, inside

the sediment, or hidden beneath the canopy of seagrass beds; these techniques were not used in our surveys. As a consequence, the list of species (228) observed in the course of the present study is certainly not exhaustive.

Several factors have been related to the distribution of fish species on coral reefs: substrate complexity, food availability, water quality, presence of current, wave exposure, available shelters, coral cover, etc. (Williams, 1991). The factors that were considered in the present study were habitat types, geographical locations of the sites, and depth. We showed that the most important factor affecting community composition is the type of habitat. Communities living on soft bottoms (seagrass beds, sandy areas, and nodule fields) were different from those living on hard substrata. Other quantitative studies carried out in the West Indies have also shown the importance of topographic complexity for the structure of fish communities (Risk, 1972; Gladfelter and Gladfelter, 1978; Luckhurst and Luckhurst, 1978; Kaufman and Ebersole, 1984; Alevizon et al., 1985). Greenfield and Johnson (1990) have shown the importance of habitat types for the structure of Blennioid communities, which are composed of cryptic and sedentary species closely associated to the seafloor.

Galzin and Legendre (1987) distinguished four assemblages for the fish communities of a Polynesian reef, which they related to different geomorphological structures: fringing reef, lagoon, reef front, and outer reef slope. In the same way, in a detailed study of reef flats in the Réunion Island, Letourneur (1996) distinguished three assemblages: back-reef, inner reef flats, and outer reef flats. This type of separation of communities in shallow areas was not found in the West Indies. Instead, a relatively homogeneous community, from a qualitative point of view, was observed from the surface to a depth of about 5 m. This can be linked to the lower level of morphologic differentiation of the lagoon and reef flat areas of Caribbean reefs, compared to those of the Indo-Pacific. However, Gladfelter and Gladfelter (1978), who analysed quantitatively the fish communities of a lagoon of Saint Croix (one of the Virgin Islands), pointed out structural variation that they linked to habitat differences. More detailed quantitative surveys, at the level of each type of reef, could reveal

more clear-cut differences between fish assemblages living in different habitats.

For outer-slope reefs, Galzin (1987) described a unique assemblage of species found between 3 and 30 m on the Tiahura site of Moorea Island (French Polynesia). On the reefs of Tulear (Madagascar), Harmelin-Vivien (1977) recognized an assemblage of species living in shallow zones and a deeper community (>20 m deep). A deep fish community was observed below 30 m on other reefs of the Indo-Pacific (Gosline, 1965; Goldman and Talbot, 1976). In the Antilles, from a qualitative point of view, two assemblages were found on reef slopes: a shallow-water and a deeper community. The upper limit of the deeper community is at about 6–8 m and its depth limit follows the limits of the reef growth (30–50 m; Bouchon-Navaro et al., 1997). From observations made with a submersible off Jamaica and off the reefs of Belize, Colin (1974) noted the presence of a deep fish community below 50 m. Dennis and Bright (1988) made observations down to 200 m; they also found that the depth limit of typical reef ichthyofauna was about 45 m in the North Western part of the Gulf of Mexico. In the present study, depth was the least important of the three groups of factors investigated. Only 1.2% of the community composition variation was explained by depth only; most of the variation explained by depth (2.7%) was also explained by habitat types. It does not mean that depth is not an important predictor of community composition; it only means that it is redundant with habitat types, which are also distributed according to depth.

The presence–absence data analysed in the present study support the hypothesis of the presence of two complementary biogeographic gradients in the West Indies: a south-to-north latitudinal gradient and a gradient along the Caribbean arch, from the Grenadines to the Dominican Republic. The polynomial Caribbean arch variables tested the hypothesis of an influence on community composition of the northward current that dominates the hydrology of the Caribbean, which is a combination of the North-Equatorial and Guiana currents. Community composition reacted in a nonlinear way to these two gradients.

These gradients were particularly noticeable for fish assemblages living below 6- to 10-m depth. The

communities found in shallow waters are more homogeneous across the Caribbean, although some differentiation is evident. From our present state of knowledge on the biogeography of the Caribbean ichthyofauna, it is difficult to provide an explanation for the gradients in community composition. A first suggestion is to search for a link with water circulation and, through it, the distribution of fish planktonic larvae. As mentioned above, the Caribbean arch is swept from south to north by the northern branch of the North-Equatorial Atlantic current. Because the richness gradient observed in the present study is caused by a larger number of species in the south, the general circulation of water, directed to the north, cannot be invoked as a cause. A study of the population genetics of some species in the Caribbean would be useful to understand the faunal migrations between islands. The gradients observed in the present study could also be due to the different types of habitat available in the different islands, as well as their different amounts of coral coverage, which could produce more or less favourable conditions for the development of juveniles (availability of food, food supply, substrate complexity with different coral cover, etc.). More detailed quantitative work on the fish fauna and other benthic communities, especially in the extreme parts of the Caribbean arch, would be necessary to study this problem.

In a study of the distribution of coastal fishes in the Western Tropical Atlantic, from the Gulf of Mexico to the South of Brazil, Robins (1971) distinguished three main zones: (1) a northern zone that stretches from Cape Canaveral on the east coast of Florida to Yucatán, including the Gulf of Mexico. The Cuban fauna and, to a lesser extent, that of Jamaica belong to that region. (2) A southern zone that includes the northern coast of Brazil, Guyana, and Venezuela to the northern portion of Columbia. (3) An intermediate zone in the middle, from Columbia to Nicaragua, where a mixture of the northern and southern ichthyofaunas is found. Concerning the insular fauna, Robins (1971) did not provide any delimitation and noted the lack of data concerning Haiti and the Dominican Republic. The southern limit of his intermediate zone is the islands of Fernando de Noronha, which may represent the southern outpost of tropical insular fauna. The Bermudan region is

considered by Robins (1971) to form a distinct biogeographic unit where a mixture of faunas coming from the Bahamas and North Carolina is found.

Three main biogeographic provinces can be recognized in the Western Atlantic region: the Bermuda province, the Caribbean province, and the Brazilian province (Briggs, 1974). After a study of the distribution of 189 fish species belonging to only nine families in the Caribbean region (United States, Bahamas, Virgin Islands, Colombia, and Venezuela), Acero (1985) showed that two subprovinces can be distinguished in the Caribbean region: (1) a northern subprovince which includes the southern portion of Florida, the Gulf of Mexico, Bermuda, the Bahamas, the Virgin Islands, as well as the continental platforms of Belize and Honduras, and (2) a southern subprovince which includes the continental coasts of Colombia and Venezuela as well as the Netherlands Antilles. Acero (1985) suggested that these two provinces could be separated at the level of San Andres Island (12°30'N). The possible eastern limit of this subprovince is still unknown. Instead of separate

subprovinces, the present study suggests the presence of a gradient. More data of the kind reported in this paper are needed to determine if this gradient runs from Venezuela all the way to Honduras, following the Caribbean arch.

### Acknowledgements

We are grateful to an anonymous reviewer who provided stimulating comments on the first draft of this manuscript. [AU]

### Appendix A

Species found in the seven islands. The species codes (right-hand column) are used in the Figures. Island codes: PV=Puerto Viejo in the Dominican Republic, AN=Anguilla, SM=Saint Martin, SB=Saint-Barthélemy, GU=Guadeloupe (GU), and BQ=Bequia in the Grenadines.

Species name	PV	AN	SM	SB	GU	MA	BQ	Abbreviation
<i>Ginglymostoma cirratum</i> (Bonnaterre, 1788)	0	0	1	0	0	0	1	Gin cir
<i>Carcharhinus limbatus</i> (Valenciennes, 1841)	0	1	0	0	0	0	0	Car lim
<i>Narcine brasiliensis</i> (Olfers, 1831)	0	0	0	0	1	0	1	Nar bra
<i>Torpedo</i> sp.	0	0	0	0	1	0	0	Tor sp
<i>Urolophus jamaicensis</i> (Cuvier, 1817)	1	0	0	0	0	0	0	Uro jam
<i>Dasyatis americana</i> Hildebrand and Schroeder, 1928	0	1	1	1	0	0	1	Das ame
<i>Aetobatus narinari</i> (Euphrasen, 1790)	0	1	1	0	0	0	0	Aet nar
<i>Gymnothorax funebris</i> Ranzani, 1840	0	0	1	0	1	0	0	Gym fun
<i>Gymnothorax moringa</i> (Cuvier, 1829)	0	1	1	1	1	1	1	Gym mor
<i>Gymnothorax vicinus</i> (Castelanau, 1855)	0	0	1	0	0	0	0	Gym vic
<i>Gymnothorax miliaris</i> (Kaup, 1856)	0	1	1	0	1	1	1	Gym mil
<i>Myrichthys breviceps</i> (Gronow, 1854)	0	0	1	0	0	1	1	Myr bre
<i>Myrichthys ocellatus</i> (LeSueur, 1821)	0	0	1	0	1	1	1	Myr oce
<i>Ophichthus ophis</i> (Linné, 1758)	0	0	0	0	1	0	0	Oph oph
<i>Heteroconger halis</i> (Böhlke, 1957)	0	0	0	0	1	0	1	Het hal
<i>Harengula humeralis</i> (Cuvier, 1829)	0	0	0	0	1	0	0	Har hum
<i>Jenkinsia lamprotaenia</i> (Gosse, 1851)	0	0	0	0	0	0	1	Jen lam
<i>Synodus intermedius</i> (Spix, 1829)	1	0	1	1	1	1	1	Syn int
<i>Synodus cf. synodus</i> (Linné, 1758)	0	0	0	0	0	1	0	Syn syn
<i>Synodus</i> sp.	0	0	0	0	0	1	0	Syn sp
<i>Ogcocephalus nasutus</i> (Cuvier and Valenciennes, 1837)	0	0	1	0	0	0	0	Ogc nas
<i>Tylosurus cf. crocodilus</i> (Peron and LeSueur, 1821)	1	1	0	0	1	1	0	Tyl cro
<i>cf. Atherinomorus stipes</i> (Müller and Troschel, 1848)	1	0	1	1	1	1	0	Ate sti
<i>Sargocentron coruscum</i> (Poey, 1860)	0	0	0	1	1	1	0	Sar cor
<i>Sargocentron vexillarium</i> (Poey, 1860)	0	0	1	0	1	1	1	Sar vex
<i>Holocentrus ascensionis</i> (Osbeck, 1765)	0	1	1	1	1	1	1	Hol asc

(continued on next page)

## Appendix A (continued)

Species name	PV	AN	SM	SB	GU	MA	BQ	Abbreviation
<i>Holocentrus rufus</i> (Walbaum, 1792)	1	1	1	1	1	1	1	Hol ruf
<i>Myripristis jacobus</i> Cuvier and Valenciennes, 1829	1	1	1	1	1	1	1	Myr jac
<i>Neoniphon marianus</i> (Cuvier, 1829)	0	0	0	0	1	1	1	Neo mar
<i>Plectrypops retrospinnis</i> (Guichenot, 1853)	0	0	0	0	1	0	0	Ple ret
<i>Aulostomus maculatus</i> Valenciennes, 1842	1	1	1	1	1	1	1	Aul mac
<i>Fistularia tabacaria</i> Linné, 1758	0	0	0	0	1	0	0	Fis tab
<i>Hippocampus</i> cf. <i>reidi</i> Ginsburg, 1933	0	0	0	0	0	1	1	Hip rei
<i>Scorpaena plumieri</i> Bloch, 1789	0	1	0	0	1	1	1	Sco plu
<i>Scorpaena</i> sp.	0	0	0	0	1	0	0	Sco sp
<i>Alphestes afer</i> (Bloch, 1793)	0	1	1	0	1	1	1	Alp afe
<i>Cephalopholis cruentatus</i> (Lacépède, 1802)	0	1	1	1	1	1	1	Cep cru
<i>Cephalopholis fulva</i> (Linné, 1758)	0	1	1	1	1	1	1	Cep ful
<i>Dermatolepis inermis</i> (Cuvier and Valenciennes, 1833)	0	1	0	0	0	0	0	Der ine
<i>Epinephelus adscensionis</i> (Osbeck, 1771)	0	1	0	1	1	1	1	Epi ads
<i>Epinephelus guttatus</i> (Linné, 1758)	0	1	1	1	1	1	1	Epi gut
<i>Epinephelus morio</i> (Cuvier and Valenciennes, 1828)	0	1	0	1	0	1	0	Epi mor
<i>Epinephelus striatus</i> (Bloch, 1792)	0	1	1	1	1	0	0	Epi str
<i>Hypoplectrus</i> cf. <i>aberrans</i> (Poey, 1868)	0	0	0	0	0	1	0	Hyp abe
<i>Hypoplectrus chlorurus</i> (Cuvier and Valenciennes, 1828)	0	1	1	1	1	1	1	Hyp chl
<i>Hypoplectrus</i> cf. <i>guttavarius</i> (Poey, 1852)	0	1	1	0	1	1	1	Hyp gut
<i>Hypoplectrus</i> cf. <i>indigo</i> (Poey, 1852)	0	1	0	0	0	0	0	Hyp ind
<i>Hypoplectrus nigricans</i> (Poey, 1852)	0	1	1	1	1	1	0	Hyp nig
<i>Hypoplectrus puella</i> (Cuvier and Valenciennes, 1828)	1	1	1	1	1	1	0	Hyp pue
<i>Hypoplectrus unicolor</i> (Walbaum, 1792)	0	1	0	0	0	1	0	Hyp uni
<i>Hypoplectrus</i> sp.1	0	0	0	0	0	1	0	Hyp sp1
<i>Hypoplectrus</i> sp.2	0	0	0	0	0	1	0	Hyp sp2
<i>Hypoplectrus</i> spp. (juvenile)	0	0	0	0	1	0	0	Hyp juv
<i>Liopropoma rubre</i> Poey, 1861	0	0	0	0	1	1	0	Lio rub
<i>Mycteroperca interstitialis</i> (Poey, 1860)	0	0	1	1	1	1	1	Myc int
<i>Mycteroperca tigris</i> (Cuvier and Valenciennes, 1833)	0	1	0	0	1	0	0	Myc tig
<i>Mycteroperca venenosa</i> (Linné, 1758)	0	1	1	1	0	0	0	Myc ven
<i>Paranthias furcifer</i> (Cuvier and Valenciennes, 1828)	0	1	0	0	1	1	1	Par fur
<i>Serranus annularis</i> (Günther, 1880)	0	0	1	0	0	0	0	Ser ann
<i>Serranus baldwini</i> (Evermann and Marsh, 1900)	0	0	1	1	1	1	1	Ser bal
<i>Serranus flaviventris</i> (Cuvier and Valenciennes, 1829)	0	0	1	0	0	1	0	Ser fla
<i>Serranus tabacarius</i> (Cuvier and Valenciennes, 1829)	1	0	1	1	1	1	1	Ser tab
<i>Serranus tigrinus</i> (Bloch, 1790)	1	1	1	1	1	1	1	Ser tig
<i>Serranus tortugarum</i> Longley, 1935	0	0	0	1	1	1	0	Ser tor
<i>Rypticus saponaceus</i> (Bloch and Schneider, 1801)	0	1	1	1	1	1	1	Ryp sap
<i>Gramma loreto</i> Poey, 1868	0	1	1	1	1	1	1	Gra lor
<i>Priacanthus arenatus</i> Cuvier, 1829	0	0	1	0	0	1	0	Pri are
<i>Heteropriacanthus cruentatus</i> (Lacépède, 1802)	0	1	1	1	1	1	1	Het cru
<i>Apogon binotatus</i> (Poey, 1867)	0	0	0	0	0	0	1	Apo bin
<i>Apogon maculatus</i> (Poey, 1861)	0	1	0	0	0	0	1	Apo mac
<i>Apogon quadrisquamatus</i> Longley, 1934	0	0	0	0	1	0	0	Apo qua
<i>Apogon townsendi</i> (Breder, 1927)	0	1	0	0	1	0	1	Apo tow
<i>Malacanthus plumieri</i> (Bloch, 1787)	0	1	1	1	1	1	1	Mal plu
<i>Echeneis naucrates</i> Linné, 1758	0	0	0	0	1	0	0	Ech nau
<i>Carangoides bartholomaei</i> (Cuvier and Valenciennes, 1833)	0	0	1	0	0	0	0	Car bar
<i>Carangoides ruber</i> (Bloch, 1793)	1	1	1	1	1	1	1	Car rub
<i>Caranx crysos</i> (Mitchill, 1815)	0	0	0	0	0	1	1	Car cry
<i>Caranx hippos</i> (Linné, 1766)	0	0	0	0	0	0	1	Car hip
<i>Caranx latus</i> Agassiz, 1829	1	0	0	0	1	1	0	Car lat
<i>Caranx lugubris</i> Poey, 1860	0	1	0	0	0	0	0	Car lug

## Appendix A (continued)

Species name	PV	AN	SM	SB	GU	MA	BQ	Abbreviation
Decapterus cf. punctatus (Cuvier, 1829)	0	0	1	0	1	0	0	Dec pun
Elagatis bipinnulatus (Quoy and Gaimard, 1824)	0	0	0	0	0	1	0	Ela bip
Oligoplites saurus (Bloch and Schneider, 1801)	0	0	0	0	0	1	0	Oli sau
Selar crumenophthalmus (Bloch, 1793)	0	1	0	0	1	0	0	Sel cru
Trachinotus goodei Jordan and Evermann, 1896	0	0	0	1	0	0	0	tra goo
Lutjanus analis (Cuvier and Valenciennes, 1828)	0	1	1	0	1	0	0	Lut ana
Lutjanus apodus (Walbaum, 1792)	1	1	1	1	1	1	1	Lut apo
Lutjanus buccanella (Cuvier, 1828)	0	0	0	0	1	0	0	Lut buc
Lutjanus cyanopterus (Cuvier and Valenciennes, 1828)	0	0	1	0	0	0	0	Lut cya
Lutjanus griseus (Linné, 1758)	1	0	1	1	1	1	0	Lut gri
Lutjanus jocu (Bloch and Schneider, 1801)	0	0	1	0	1	1	0	Lut joc
Lutjanus mahogoni (Cuvier and Valenciennes, 1828)	0	1	1	1	1	1	1	Lut mah
Lutjanus synagris (Linné, 1758)	0	0	1	1	1	1	0	Lut syn
Ocyurus chrysurus (Bloch, 1791)	1	1	1	1	1	1	1	Ocy chr
Diapterus rhombeus (Cuvier, 1829)	0	0	0	0	0	1	0	Dia rho
Gerres cinereus (Walbaum, 1792)	1	1	1	1	1	1	0	Ger cin
Eucinostomus sp.	0	0	0	0	0	0	1	Euc sp
Anisotremus surinamensis (Bloch, 1791)	0	1	0	1	1	0	1	Ani sur
Anisotremus virginicus (Linné, 1758)	0	0	1	1	1	0	0	Ani vir
Haemulon album Cuvier, 1829	0	0	0	0	0	0	1	Hae alb
Haemulon aurolineatum Cuvier, 1829	1	1	1	1	1	1	1	Hae aur
Haemulon bonariense Cuvier, 1829	0	0	0	0	1	1	0	Hae bon
Haemulon carbonarium Poey, 1860	0	1	1	1	1	1	1	Hae car
Haemulon chrysargyreum Günther, 1859	1	1	1	1	1	1	1	Hae chr
Haemulon flavolineatum (Desmarest, 1823)	1	1	1	1	1	1	1	Hae fla
Haemulon macrostomum Günther, 1859	0	0	1	0	1	0	0	Hae mac
Haemulon melanurum (Linné, 1758)	0	0	0	0	0	1	1	Hae mel
Haemulon parra (Desmarest, 1823)	0	0	1	0	0	0	1	Hae par
Haemulon plumieri (Lacépède, 1802)	1	1	1	1	1	1	0	Hae plu
Haemulon sciurus (Shaw, 1803)	1	1	1	1	1	1	0	Hae sci
Inermia vittata Poey, 1861	0	1	1	0	1	1	0	Ine vit
Calamus bajonado (Bloch and Schneider, 1801)	0	1	1	1	1	0	0	Cal baj
Calamus calamus (Cuvier and Valenciennes, 1830)	0	0	1	1	1	0	0	Cal cal
Calamus pennatula Guichenot, 1868	0	1	1	1	0	0	1	Cal pen
Equetus acuminatus (Bloch and Schneider, 1801)	0	1	1	1	1	1	0	Equ acu
Equetus lanceolatus (Linné, 1758)	0	0	0	0	0	1	0	Equ lan
Equetus punctatus (Bloch and Schneider, 1801)	1	0	1	1	1	1	1	Equ pun
Odontoscion dentex (Cuvier, 1830)	0	0	0	0	0	1	1	Odo den
Umbrina coroides (Cuvier, 1830)	0	0	0	0	0	1	0	Umb cor
Mulloidichthys martinicus (Cuvier, 1829)	1	1	1	1	1	1	1	Mul mar
Pseudupeneus maculatus (Bloch, 1793)	1	1	1	1	1	1	1	Pse mac
Pempheris scomburgki Müller and Troschel, 1848	1	1	1	1	1	1	1	Pem sco
Kyphosus sectatrix (Linné, 1758)	1	1	1	1	1	1	1	Kyp sec
Chaetodipterus faber (Broussonet, 1782)	0	0	0	0	1	1	0	Cha fab
Chaetodon aculeatus (Poey, 1860)	0	0	0	0	1	1	1	Cha acu
Chaetodon capistratus Linné, 1758	1	1	1	1	1	1	1	Cha cap
Chaetodon ocellatus Bloch, 1787	0	0	0	0	0	1	1	Cha oce
Chaetodon sedentarius Poey, 1860	0	1	1	1	1	1	1	Cha sed
Chaetodon striatus Linné, 1758	0	1	1	1	1	1	1	Cha str
Centropyge argi Woods and Kanazawa, 1951	0	0	0	0	0	1	1	Cen arg
Holacanthus ciliaris (Linné, 1758)	0	1	1	1	1	1	1	Hol cil
Holacanthus tricolor (Bloch, 1795)	1	1	1	1	1	1	1	Hol tri
Pomacanthus arcuatus (Linné, 1758)	0	1	1	1	0	0	0	Pom arc

(continued on next page)

## Appendix A (continued)

Species name	PV	AN	SM	SB	GU	MA	BQ	Abbreviation
<i>Pomacanthus paru</i> (Bloch, 1787)	0	1	1	1	1	1	1	Pom par
<i>Abudefduf saxatilis</i> (Linné, 1758)	1	1	1	1	1	1	1	Abu sax
<i>Abudefduf taurus</i> (Müller and Troschel, 1848)	1	1	1	1	0	1	1	Abu tau
<i>Chromis cyanea</i> (Poey, 1860)	1	1	1	1	1	1	1	Chr cya
<i>Chromis cf. insolata</i> (Cuvier, 1830)	0	0	0	0	1	0	0	Chr ins
<i>Chromis multilineata</i> (Guichenot, 1853)	1	1	1	1	1	1	1	Chr mul
<i>Microspathodon chrysurus</i> (Cuvier, 1830)	1	1	1	1	1	1	1	Mic chr
<i>Stegastes diencaeus</i> Jordan and Rutter, 1898	1	1	1	1	1	1	0	Ste die
<i>Stegastes dorsopunicans</i> (Poey, 1867)	1	1	1	1	1	1	1	Ste dor
<i>Stegastes cf. fuscus</i> (Cuvier and Valenciennes, 1830)	0	0	1	0	1	1	0	Ste fus
<i>Stegastes leucosticus</i> (Müller and Troschel, 1848)	1	1	1	1	1	1	0	Ste leu
<i>Stegastes partitus</i> (Poey, 1867)	1	1	1	1	1	1	1	Ste par
<i>Stegastes planifrons</i> (Cuvier and Valenciennes, 1830)	1	1	1	1	1	1	1	Ste pla
<i>Stegastes variabilis</i> (Castelnaud, 1855)	1	1	1	1	1	1	0	Ste var
<i>Stegastes sp.1</i>	0	0	0	0	1	0	0	Ste sp1
<i>Stegastes sp.2</i>	0	0	0	0	0	1	0	Ste sp2
<i>Stegastes sp.3</i>	0	0	0	0	0	1	0	Ste sp3
<i>Amblycirrhitus pinos</i> (Mowbray, 1927)	1	0	1	0	1	1	1	Amb pin
<i>Mugil sp.</i>	0	0	1	0	0	0	0	Mug sp
<i>Sphyræna barracuda</i> (Walbaum, 1792)	1	1	1	1	1	1	1	Sph bar
<i>Sphyræna guachancho</i> Cuvier, 1829	0	0	1	0	1	0	0	Sph gua
<i>Bodianus rufus</i> (Linné, 1758)	1	1	1	1	1	1	1	Bod ruf
<i>Clepticus parrae</i> (Bloch and Schneider, 1801)	0	1	1	1	1	1	1	Cle par
<i>Doratonotus megalepis</i> Günther, 1862	0	0	0	0	0	0	1	Dor meg
<i>Halichoeres bivittatus</i> (Bloch, 1791)	1	0	1	1	1	1	1	Hal biv
<i>Halichoeres cyanocephalus</i> (Bloch, 1791)	0	1	0	0	0	1	1	Hal cya
<i>Halichoeres gamoti</i> (Cuvier and Valenciennes, 1839)	1	1	1	1	1	1	1	Hal gar
<i>Halichoeres maculipinna</i> (Müller and Troschel, 1848)	1	1	1	1	1	1	1	Hal mac
<i>Halichoeres pictus</i> (Poey, 1860)	0	0	0	0	1	0	0	Hal pic
<i>Halichoeres poeyi</i> (Steindachner, 1867)	1	1	1	1	1	1	1	Hal poe
<i>Halichoeres radiatus</i> (Linné, 1758)	0	1	1	1	1	1	1	Hal rad
<i>Halichoeres sp.</i>	0	0	0	0	0	1	0	Hal sp
<i>Lachnolaimus maximus</i> (Walbaum, 1792)	0	0	0	0	1	1	0	Lac max
<i>Thalassoma bifasciatum</i> (Bloch, 1791)	1	1	1	1	1	1	1	Tha bif
<i>Xyrichtys martinicensis</i> (Valenciennes, 1839)	0	0	0	0	1	1	1	Xyr mar
<i>Xyrichtys splendens</i> Castelnaud, 1855	0	0	0	1	1	0	1	Xyr spl
<i>Cryptotomus roseus</i> Cope, 1871	0	0	0	1	1	0	0	Cry ros
<i>Scarus coelestinus</i> Cuvier and Valenciennes, 1839	0	1	0	0	0	0	0	Sca cel
<i>Scarus coeruleus</i> (Bloch, 1786)	0	0	0	1	0	0	0	Sca coe
<i>Scarus guacamaia</i> Cuvier, 1829	0	0	0	0	1	0	0	Sca gua
<i>Scarus iserti</i> Bloch, 1789	1	1	1	1	1	1	1	Sca ise
<i>Scarus taeniopterus</i> Desmarest, 1831	1	1	1	1	1	1	1	Sca tae
<i>Scarus vetula</i> Bloch and Schneider, 1801	1	1	1	1	1	0	1	Sca vet
<i>Scarus sp.1</i> (juvenile)	0	0	0	0	0	1	0	Sca sp1
<i>Sparisoma atomarium</i> (Poey, 1861)	0	0	1	1	1	1	0	Spa ato
<i>Sparisoma aurofrenatum</i> (Cuvier and Valenciennes, 1839)	1	1	1	1	1	1	1	Spa aur
<i>Sparisoma chrysopterum</i> (Bloch and Schneider, 1801)	1	1	1	1	1	1	0	Spa chr
<i>Sparisoma radians</i> (Cuvier and Valenciennes, 1839)	1	0	1	1	1	1	1	Spa rad
<i>Sparisoma rubripinne</i> (Cuvier and Valenciennes, 1839)	1	1	1	1	1	1	1	Spa rub
<i>Sparisoma viride</i> (Bonnaterre, 1788)	1	1	1	1	1	1	1	Spa vir
<i>Sparisoma sp.</i> (juvenile)	0	0	0	0	0	1	0	Spa sp
<i>Opistognathus aurifrons</i> (Jordan and Thompson, 1905)	0	0	0	0	1	1	0	Opi aur
<i>Labrisomus nuchipinnis</i> (Quoy and Gaimard, 1824)	0	0	1	0	1	0	1	Lab nuc
<i>Labrisomus cf. gobio</i> (Valenciennes)	0	0	1	0	1	0	0	Lab gob

## Appendix A (continued)

Species name	PV	AN	SM	SB	GU	MA	BQ	Abbreviation
Malacoctenus sp.	0	1	1	0	1	0	1	Mal sp
Paraclinus cf. fasciatus (Steindachner, 1876)	1	0	0	0	0	0	0	Par fas
Acanthemblemaria sp.	0	0	0	0	1	0	0	Aca sp
Chaenopsis sp.	1	0	0	0	0	0	0	Cha sp
Ophioblennius atlanticus (Cuvier and Valenciennes, 1836)	1	1	1	1	1	1	1	Oph atl
Paradiplogrammus bairdi Jordan, 1887	0	0	0	0	1	1	1	Par bai
Coryphopterus dicrus Böhlke and Robins, 1968	1	0	0	1	1	0	0	Cor dic
Coryphopterus cf. eidolon Böhlke and Robins, 1960	0	0	0	0	1	0	0	Cor eid
Coryphopterus glaucofraenum Gill, 1863	0	0	1	1	1	1	1	Cor gla
Coryphopterus lipernes Böhlke and Robins, 1962	0	0	0	0	1	1	1	Cor lip
Coryphopterus personatus (Jordan and Thompson, 1905)	0	0	1	1	1	1	0	Cor per
Gnatholepis thompsoni Jordan, 1902	0	0	0	1	1	0	0	Gna tho
Gobiosoma cf. evelynae Böhlke and Robins, 1968	0	1	1	1	1	1	1	Gob eve
Ioglossus cf. helenae Randall, 1968	0	0	0	0	1	1	0	Iog hel
Acanthurus bahianus Castelnau, 1855	1	1	1	1	1	1	1	Aca bah
Acanthurus chirurgus (Bloch, 1787)	1	1	1	1	1	1	1	Aca chi
Acanthurus coeruleus Bloch and Schneider, 1801	1	1	1	1	1	1	1	Aca coe
Scomberomorus cavalla (Cuvier, 1829)	0	1	0	0	0	1	0	Sco cav
Scomberomorus regalis (Bloch, 1793)	0	0	0	1	1	1	1	Sco reg
Bothus lunatus (Linné, 1758)	0	0	1	0	1	1	1	Bot lun
Bothus ocellatus (Agassiz, 1831)	0	1	1	0	0	1	0	Bot oce
Aluterus monoceros (Linné, 1758)	0	0	0	0	1	0	0	Alu mon
Aluterus cf. schoepfi (Walbaum, 1792)	0	0	0	0	1	0	0	Alu sch
Aluterus scriptus (Osbeck, 1765)	0	0	1	1	1	0	1	Alu scr
Balistes vetula Linné, 1758	0	1	1	1	1	1	1	Bal vet
Cantherhines macrocerus (Hollard, 1854)	0	1	0	1	1	0	0	Can mac
Cantherhines pullus (Ranzani, 1842)	0	1	1	1	1	1	1	Can pul
Canthidermis sufflamen (Mitchill, 1815)	0	1	0	0	0	0	0	Can suf
Melichthys niger (Bloch, 1786)	0	1	1	0	1	1	1	Mel nig
Monacanthus ciliatus (Mitchill, 1818)	0	0	0	0	1	0	1	Mon cil
Monacanthus tuckeri Bean, 1906	0	1	1	1	0	1	1	Mon tuc
Stephanolepis setifer (Bennett, 1830)	0	0	1	0	0	1	0	Ste set
Acanthostracion polygonius Poey, 1876	0	1	1	1	1	0	1	Aca pol
Acanthostracion quadricornis (Linné, 1758)	0	1	1	0	1	0	1	Aca qua
Lactophrys bicaudalis (Linné, 1758)	0	0	0	1	1	1	1	Lac bic
Lactophrys trigonus (Linné, 1758)	0	1	1	0	1	0	1	Lac tri
Lactophrys triqueter (Linné, 1758)	0	1	1	1	1	1	1	Lac trq
Canthigaster rostrata (Bloch, 1782)	1	1	1	1	1	1	1	Can ros
Sphoeroides greeleyi (Gilbert, 1900)	0	0	0	0	0	1	0	Sph gre
Sphoeroides spengleri (Bloch, 1785)	0	1	1	1	1	1	1	Sph spe
Cyclichthys antennatus (Cuvier, 1818)	0	0	0	1	1	0	0	Cyc ant
Cyclichthys antillarum Jordan and Rutter, 1897	0	0	0	1	1	0	0	Cyc anl
Diodon holacanthus Linné, 1758	0	0	1	0	1	1	1	Dio hol
Diodon hystrix Linné, 1758	0	1	1	0	1	1	0	Dio hys

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