

Spatial and Temporal Variation in a Caribbean Herbivorous Fish Assemblage

Dorothee Kopp[†], Yolande Bouchon-Navaro[†], Max Louis[†], Pierre Legendre[‡],
and Claude Bouchon[†]

[†]DYNECAR

Laboratoire de Biologie Marine
Université des Antilles et de la Guyane
97159 Pointe-à-Pitre Guadeloupe
dkopp@univ-ag.fr

[‡]Département de Sciences Biologiques

Université de Montréal
C.P. 6128, Succursale Centre-Ville
Montréal, Québec H3C3J7, Canada



www.cerf-jcr.org

ABSTRACT

KOPP, D.; BOUCHON-NAVARO, Y.; LOUIS, M.; LEGENDRE, P., and BOUCHON, C., 2012. Spatial and temporal variation in a Caribbean herbivorous fish assemblage. *Journal of Coastal Research*, 28(1A), 63–72. West Palm Beach (Florida), ISSN 0749-0208.

The present work analyses the spatial and temporal variations of the herbivorous fish assemblage on 10 coral reef sites in the Caribbean island of Guadeloupe (French West Indies). The herbivorous fish assemblage was assessed by visual census along band transects; environmental data were collected to determine the relationship between environmental conditions and temporal and spatial variations in herbivorous fish abundance and distribution. Spatial variation in species abundance was related to variation of the benthic cover (*e.g.*, coral and algae), depth, and protection status among sites. Short-term fluctuations of herbivorous fishes on the reef flats were linked to tide, swell, and wind, whereas long-term variations were seasonal and highly correlated to annual water temperature oscillations.

ADDITIONAL INDEX WORDS: *Canonical redundancy analysis (RDA), coral reefs, principal coordinates of neighbor matrices (PCNM), spatiotemporal variations.*



www.JCRonline.org

INTRODUCTION

The combined effects of overfishing and nutrient enrichment have been labeled as major contributors for the decline of coral reef fauna worldwide (Jackson *et al.*, 2001). Intense harvesting of herbivorous fish combined with anthropogenic nutrient enrichment result in a phase shift from coral- to algae-dominated reefs (Hughes, 1994; Hughes *et al.*, 2003, 2007a, 2007b; Lapointe, 1997; Mumby *et al.*, 2006; Pandolfi *et al.*, 2003).

Coral cover on Caribbean reefs has dramatically declined during the last decade (Gardner *et al.*, 2003; Wilkinson and Souter, 2008). Corals have undergone phase shifts to alternate degraded assemblages because of the combined effects of overfishing (Hughes, 1994; Jackson *et al.*, 2001), pollution (Lapointe, 1997; McClanahan *et al.*, 2005), increased sedimentation (Munday, 2004), and the direct and indirect impacts of climate change (Hughes *et al.*, 2003). In the French West Indies, coral reefs, which were originally flourishing, are now experiencing a phase shift to algal dominance. Coral communities have declined and have been supplanted by algal communities dominated by brown macroalgae such as *Dicthyota*, *Lobophora*, and *Sargassum* (Bouchon *et al.*, 2008). Previous studies have shown that herbivorous organisms are able to regulate algal growth on coral reefs (Hughes *et al.*,

2007a, 2007b; Mumby *et al.*, 2006; Paddock, Cowen, and Sponaugle, 2006). It is thus of interest to determine the spatial and temporal scales that influence how herbivorous fish assemblages are structured on coral reefs. Indeed, coral reef fish show fluctuations on several spatiotemporal scales (Galzin, 1987a, 1987b; Letourneur, 1996a, 1996b; Williams, 1991). Many types of distribution patterns exist for reef fish over a wide range of spatial scales (Williams, 1991). The spatial distribution of coral reef species may vary at small scale, depending on several factors, such as habitat characteristics (*e.g.*, live coral cover, topography complexity, vertical relief, and availability of shelter), competition, predation, anthropogenic pressure, and hydrodynamic conditions. Assemblage structure may also vary over greater spatial scales depending on other factors, such as larval settlement. Some studies provide data about temporal variations of coral reef fish (Bouchon-Navaro, 1997; Galzin, 1987b; Letourneur, 1996b; Williams, 1983) and showed that the different assemblages varied at different temporal scales (*i.e.*, day or season), but none of these studies have focused specifically on the Caribbean herbivorous fish assemblages.

In this study, we focused on the coral reefs of Guadeloupe, which are subjected to both human influence and climatic changes (Bouchon *et al.*, 2008). Assuming that these factors increase the chance of successful invasion by macroalgae, we hypothesized that herbivorous fishes, regulating these algal assemblages, would differ in their responses to spatial (*e.g.*, depth, algal cover, or protection status) and temporal (*e.g.*,

DOI: 10.2112/JCOASTRES-D-09-00165.1 received 29 November 2009; accepted in revision 15 May 2010.

Published Pre-print online 18 August 2010.

© Coastal Education & Research Foundation 2012

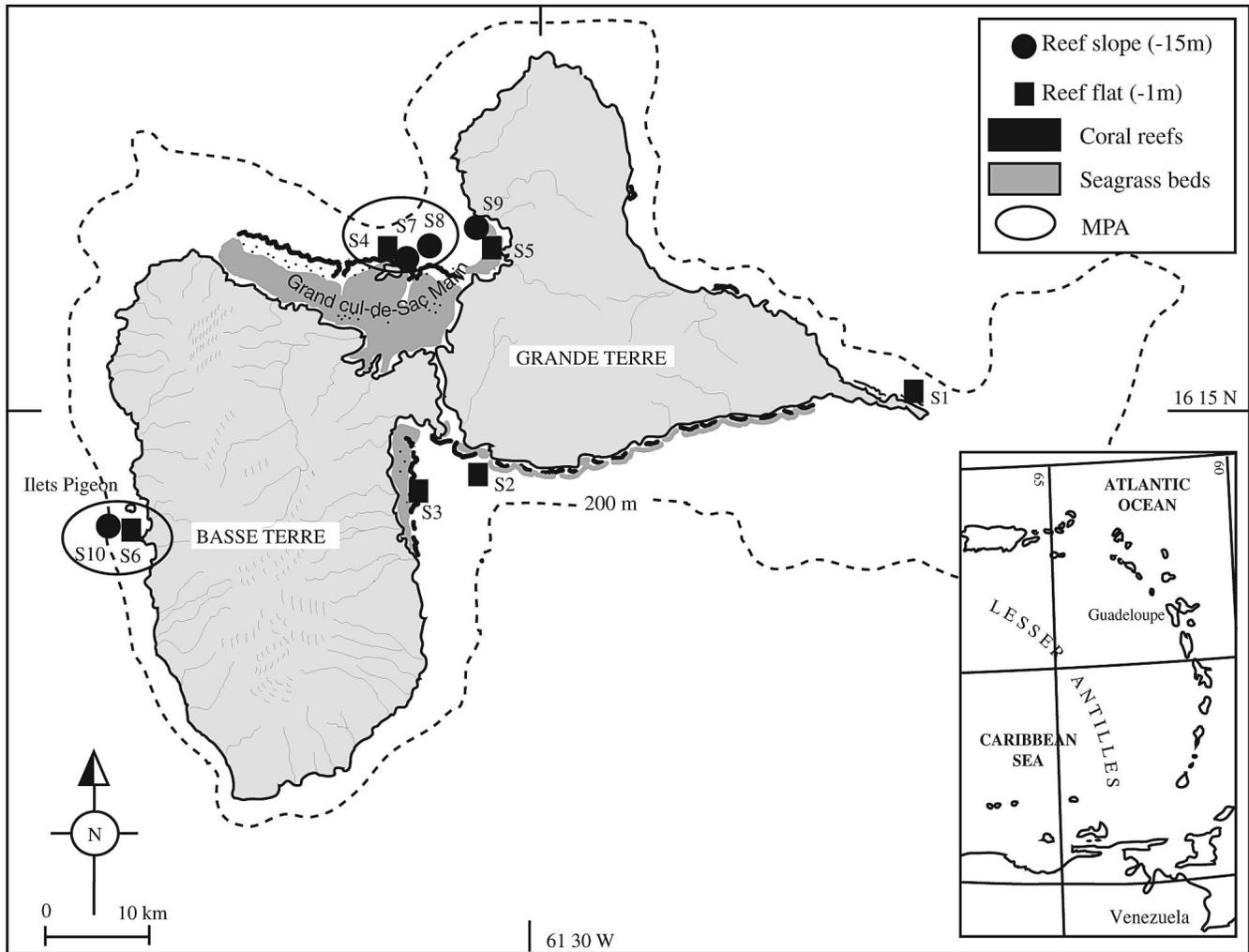


Figure 1. Map of the study area and location of the study sites.

season and tide) variables. Our first objective was to ascertain whether herbivorous fish exhibited distinct distribution patterns across reef flats and outer reef slopes. Second, we sought to model short- and long-term temporal variations of the herbivorous fish abundance and to identify the environmental variables responsible for these variations.

MATERIALS AND METHODS

To address these questions, visual censuses were conducted during the dry and rainy seasons in different coral reefs of Guadeloupe Island, located either on reef slopes or on reef flats; the reefs differed mainly by their depth and cover characteristics. The temporal patterns were estimated in one reef flat by visual censuses during an 18-month period.

Study Area

Guadeloupe is located in the eastern Caribbean Sea at 16°15' N, 61°35' W (Figure 1). Coral reefs are in high abundance

around the island; some of them have been protected since the 1980s. On protected reefs, human activities like fishing, diving, and anchoring are restricted and often forbidden (Guadeloupe National Park, 2005). The Guadeloupe marine protected areas (MPAs) studied are located around Ilets Pigeon (400 ha) on the western coast and in the bay of the Grand Cul-de-Sac Marin (2135 ha) in the north of the islands. The climate in Guadeloupe is typical of tropical areas, with a dry and a rainy season. Around Guadeloupe, mean water temperature varies throughout the year from 25.8 to 29.9°C, with minimum temperature during the dry season and maximum during the rainy season. Water salinity is 35.5 psu. The sampling areas were not under the influence of freshwater discharges; nutrient concentrations of nitrate and phosphate are very low—respectively, under 0.05 and 0.02 $\mu\text{mol}\cdot\text{L}^{-1}$ (Kopp, 2007).

Spatial and Temporal Patterns

Among the studied sites, six reef flats (S1–S6) (Figure 1) located at a 1-m depth and four reef slopes (S7 to S10)

between a 10- and a 15-m depth were surveyed twice during 2004. One sampling occurred during the dry season (June–July) and one during the rainy season (November–December) to enable seasonal comparisons. One reef flat (S4) was chosen to study the temporal variation of the herbivorous fish assemblage and sampled monthly from January 2004 to June 2005. S4 was selected because it is located inside MPA, so the observed variations could be attributed only to environmental conditions and not to fishing activities. Finally, to better understand the distribution of the herbivorous fish assemblage according to depth, one of the reef slopes (S10) was sampled during the rainy season at different depths (3, 10, 15, 20, and 30 m). This site was chosen for the same reason as S4 and because it was the only site easily accessible to 30 m.

Visual Census

The herbivorous fish assemblage was studied using visual censuses by scuba diving. Estimates of fish abundances, both in density and biomass, were obtained from two replicates of 150×2 m band transects. The strip transect technique is the most frequently used for ecological studies of reef fish assemblages (Bellwood and Alcala, 1988). Seven species of Scaridae (genera *Scarus* and *Sparisoma*), three species of Acanthuridae (genus *Acanthurus*), and the Blennidae species *Ophioblennius atlanticus* are present in Guadeloupe. At the same time, a second observer recorded the whole fish community. Care was taken not to recensus fish already counted. All individuals observed in the band transects were identified to species and noted with an estimate of their sizes. Lengths were grouped in 5-cm size classes for fish up to 20 cm and 10-cm size classes for fish larger than 20 cm. Fish biomass was then estimated using the median value of each class and weight–length relationships available in the literature (Bohnsack and Harper, 1988; Bouchon-Navaro, 1997; Claro and García-Arteaga, 1994). Accuracy of fish length estimation was maintained by practicing with object of known length at intervals throughout the study period. All the counts were conducted by the same observers (D. Kopp for the herbivorous fish assemblage and Y. Bouchon-Navaro for the whole fish community). Prior to the study, fish count results (23 samplings) for both observers were compared using nonparametric Wilcoxon tests. Tests were realized on species richness, abundance, and biomass of herbivorous fish and revealed that there was no significant difference between both observers.

As we wished to study the temporal variations of herbivorous fishes, it seemed pertinent to consider young recruits that established on the reefs. That is why we decided to separate fish under 5 cm from the other individuals. This size class was determined according to the literature. Indeed for Robertson (1988), acanthurids establishment occurs at a size between 26.9 and 26.7 mm. Concerning scarids, Bellwood and Choat (1989) determined that juvenile establishment occurs at a size between 2 and 10% of the maximal size of the individuals (corresponding to sizes inferior to 5 cm for the present scarid species).

Environmental Variables

For the study of the temporal variations, 10 environmental variables were measured each time site S4 was visited. These variables were (1) algal turf cover (%), (2) tide height (m), (3) water transparency (m), (4) rainfall ($\text{mm}\cdot\text{h}^{-1}$), (5) cloud cover (%), (6) water temperature ($^{\circ}\text{C}$), (7) daily global radiance ($\text{J}\cdot\text{cm}^{-2}$), (8) swell height (m), (9) wind speed (knots), and (10) wind orientation (northeasterly, easterly, or southeasterly). All these variables reflected the conditions during the sampling periods. Only the rainfall was considered as the mean during the month before the sampling. Indeed, it might be a lag between the rainfall that is likely to affect water clarity and its influence on fish assemblages. Meteorological data were supplied by a meteorological station upwind from site S4 (Météo France, Raizet Airport). The tide values were calculated with the model supplied by the Service Hydrologique et Océanographique de la Marine (2010). Water transparency was measured horizontally using a Secchi disc.

For the spatial study, each time a site was visited, 14 environmental variables were measured. These variables were benthic coverage (%) of (1) algal turf, (2) Cyanobacteria, (3) soft Chlorophyta, (4) calcareous Chlorophyta, (5) Phaeophyta, (6) erected Rhodophyta, (7) encrusting coralline algae, (8) coral, and (9) other benthic invertebrates like sponges and gorgonians; different substrate types (%) for (10) rock, (11) coral rubble, and (12) sand; (13) depth (m); and (14) protection status (MPA or not).

Benthic community surveys were used to estimate the total percent composition of the benthos at each site. They were conducted simultaneously with the fish surveys using a linear point intercept sampling (Lucas and Seber, 1977). The substratum types (*i.e.*, rock, coral rubble, and sand) and the quantitative composition of the benthic community were recorded beneath each 1-m mark distributed every meter along the 150-m long transect. Therefore, the percent coverage of each substratum type and benthic species were estimated from 150 point counts.

Data Analyses

Fish assemblage characteristics (species richness, number of individuals, and biomass) between reef flats and reef slopes were compared using Mann-Whitney U tests in which the null hypothesis was the absence of site effects (reef flat or slope).

The herbivorous fish data was related to environmental variables using canonical redundancy analyses (RDA) (Rao, 1964). This canonical technique was used to relate a matrix of species or other response variables (Y) to a corresponding matrix of environmental or other explanatory variables (X) (Legendre and Legendre, 1998). RDAs were performed using the CANOCO program (ter Braak and Šmilauer, 2002). Results of the ordination were displayed in correlation triplots. The axes were scaled by adjusting the species scores to the species variance; the resulting scores are correlations between the species and the eigenvectors (ter Braak, 1990). The additional contribution of each environmental variable to the RDA model was evaluated by Monte Carlo permutation tests during

forward selection of the explanatory variables at the 0.05% significance level (999 permutations).

As recommended by Legendre and Birks (2010), canonical ordinations were used as a form of time-series analysis for multivariate ecological response data. The fish dataset covers 18 months. Principal coordinates of neighbor matrices (PCNM) (Borcard and Legendre, 2002) were used to analyze the temporal structure in the multivariate fish data. Significant PCNM variables can be represented alone or assembled into submodels that correspond to different temporal scales present in the data. PCNM variables were created using the “pcnm” function that is part of the Spacemaker R-language library (Dray, Legendre, and Peres-Netos, 2006). They were subjected to forward selection against the transformed fish data, using the forward.sel function of the Packfor library (Dray, 2005). PCNM variables were selected by Monte Carlo permutation tests (9999 permutations). These PCNMs were then used as explanatory variables in RDA using the R function “rdaTest” (Legendre and Durand, 2009). Following Legendre and Gallagher (2001), the multivariate species data were Hellinger-transformed prior to the multivariate (multispecies) analyses (RDA and PCNM).

Finally, Kendall rank correlations were performed to search for correlations between environmental variables and fish temporal variations.

RESULTS

Spatial Distribution

Herbivorous Fish Assemblage

Species richness varied from 6 and 10 on reef flats (mean 8.8 species) and from 6 to 9 on reef slopes (mean 7.5) (Table 1). On reef flats, *Scarus iserti*, *Sparisoma rubripinne*, *Sp. viride*, *Acanthurus bahianus*, and *A. coeruleus* were present at all sites. On reef slopes, *Sp. viride*, *A. bahianus*, and *A. coeruleus* were present too, but *Sp. rubripinne* and *Sc. iserti* were replaced by *Sc. taeniopterus* and *Sp. aurofrenatum*.

Concerning the abundance data, Table 1 shows that herbivores were significantly more abundant on reef flats

(mean 75.0 ind.100 m⁻²) than on reef slopes (mean 46.0 ind.100 m⁻²) ($p = 0.014$). Herbivore biomass did not, however, significantly differ between reef flats and reef slopes ($p = 0.415$).

Scarid abundance did not differ between the two habitats (Table 1; $p = 0.496$) with equivalent abundances on reef flats and reef slopes (respectively, 32.9 ± 3.0 and 34.4 ± 1.8 ind.100 m⁻²). Acanthurids displayed significant higher densities on the reef flats than on the reef slopes ($p < 0.001$).

Scarid biomass are significantly higher on reef slopes than on reef flats (Table 1; $p = 0.394$) whereas the contrary was observed for Acanthuridae.

Herbivorous Fish Assemblage and Environmental Variables

Canonical RDA showed that the environmental variables explained 52.9% of the variation in the species abundance data (Figure 2a). An overall permutation test of significance showed that the canonical R^2 between herbivore abundances and environmental factors was highly significant ($p = 0.001$). The first two canonical axes explained 45.2% of the variation in the species data and 79.3% of the species–environment relationship. Six environmental variables had a significant influence on numbers of individuals: coral cover, other benthic invertebrates cover, algal cover, sand, rubble, and depth. The depth axis separates the reef flats from the reef slopes, with the S10 samples (3, 10, 15, 20, and 30 m) distributed along the depth gradient. The analysis showed that three species of scarids were more numerous on reef slopes (*Scarus taeniopterus*, *Sp. aurofrenatum* and *Sp. viride*) whereas *Sp. chrysopterus* and *Sc. iserti* were more abundant on reef flats. *Sc. taeniopterus* presents more individuals in areas where the coral cover was important. *Sc. iserti* seemed to prefer the sandy substrate whereas *Sp. rubripinne* was found in high numbers on coral rubble (Figure 2a).

For the biomass data (Figure 2b), RDA showed that the environmental variables explained 50.9% of the variation in the species data. The relationship was highly significant ($p = 0.001$). The first two canonical axes explained 42.5% of the variation in the species biomass data and 79.6% of the species–environment relationship. Among the 14 environmental factors included in the analysis, 5 had a significant influence on the biomass data: Phaeophyta cover, Rhodophyta cover, coral covers, depth, and protection status. Depth influenced the herbivorous fish assemblages, separating reef slopes from reef flats, with S10 sites distributed along the depth vector. Large individuals of *Sp. viride* and *Sp. aurofrenatum* were preferentially observed in deep areas. Areas with high coral covers, which coincided with the MPA, harbored large individuals of *Sc. taeniopterus*. *Sc. iserti*, *Sp. chrysopterus*, and *A. chirurgus* showed high biomass outside the MPA, on degraded reef flats and reef slopes. Macroalgal cover also had an influence on herbivore assemblages. Large individuals of *Sp. rubripinne* preferred Phaeophyta cover, whereas *A. coeruleus*, *A. bahianus* and *Ophioblennius atlanticus* were related to Rhodophyta cover (Figure 2b).

Table 1. Comparison of the herbivorous fish assemblage variables between reef flats and reef slopes.*

Assemblage Characteristic	Reef Flats	Reef Slopes	U Value	p Value†
Species Number	8.8 (0.3)	7.5 (0.3)	32.5	0.011
Assemblage	75.0 (2.3)	46.0 (1.2)	123.0	0.014
Scaridae	32.9 (3.0)	34.4 (1.8)	90.5	0.496
Acanthuridae	38.1 (4.2)	11.6 (1.4)	143.0	<0.001
Biomass				
Assemblage	3627 (53)	4722 (144)	63.0	0.415
Scaridae	1785 (61)	3697 (227)	39.0	0.034
Acanthuridae	1442 (53)	953 (80)	96.0	0.328

* Values are in mean number.100 m⁻² for the abundance and in mean g.100 m⁻² concerning biomass. Standard error of the mean is in parentheses. Statistical results from Mann-Whitney U tests.

† Significant results are in bold.

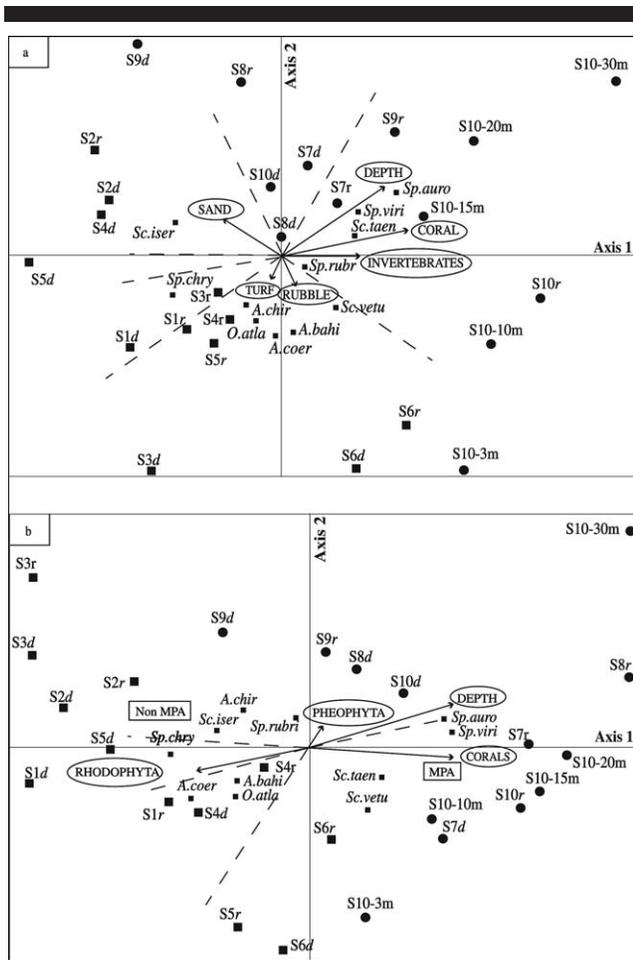


Figure 2. Correlation biplot based on a RDA ordination of the herbivore abundances (a) and biomass (b) constrained by the environmental variables. Only the environmental factors retained by forward selection ($p < 0.05$) are shown. Quantitative variables are circled and indicated by arrows and qualitative are framed. *d* = dry season, *r* = rainy season, ● = reef slopes, ■ = reef flats. *A.bahi* = *Acanthurus bahianus*, *A.chir* = *Acanthurus chirurgus*, *A.coer* = *Acanthurus coeruleus*, *O.atla* = *Ophioblennius atlanticus*, *Sc.iser* = *Scarus iserti*, *Sc.taen* = *Scarus taeniopterus*, *Sc.vetu* = *Scarus vetula*, *Sp.auro* = *Sparisoma aurofrenatum*, *Sp.chry* = *Sparisoma chrysopterygus*, *Sp.rubr* = *Sparisoma rubripinne*, *Sp.viri* = *Sparisoma viride*.

Temporal Variations

Short-Term Variations

Canonical RDA was carried out on synthetic descriptors of the herbivorous assemblages, *i.e.*, species richness, number of individuals, biomass, proportion of herbivores in number and biomass among the whole fish community, the Shannon diversity index computed on abundance and biomass data, and the equitability in abundance and biomass. The first two factorial axes explained 51.3% of the variance of the data, with 40.1% for axis 1 and 11.2% for axis 2. Three environmental variables were significant: swell, tide, and easterly winds. Examination of the correlation coefficients and canonical coefficients showed that the first axis is mostly explained by

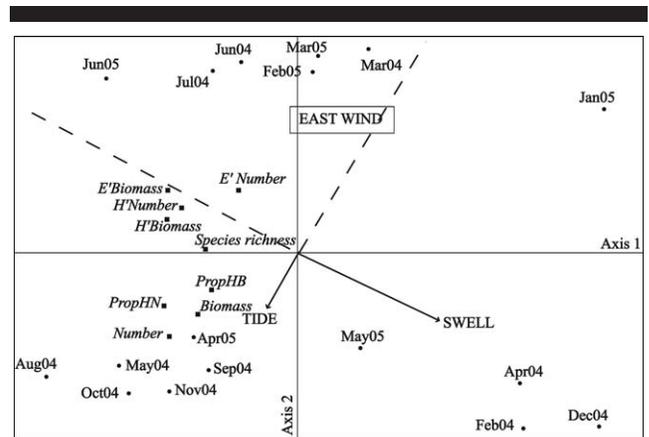


Figure 3. Correlation biplot of the RDA ordination of descriptors of the herbivorous fish assemblage constrained by the environmental variables. Only the environmental factors retained by forward selection ($p < 0.05$) are shown. Quantitative variables are indicated by arrows; qualitative variables are framed. PropHN = proportion of herbivores in number, PropHB = proportion of herbivores in biomass, H'Number = Shannon diversity index computed on abundance, H'Biomass = Shannon diversity index computed on biomass data, E'Number = equitability in abundance, E'Biomass = equitability in abundance.

swell ($r = 0.85$) and axis 2 by wind ($r = 0.98$). Results show that tidal state had an influence on the abundance and biomass of fish (Figure 3). The diversity and equitability indices were also opposed to the swell vector. Species richness and fish diversity were more important on the reef flat when the sea is calm. The easterly winds, which generate a choppy sea, had the same negative effect on fish distribution in shallow water.

Projection of the month records in Figure 3 showed that axis 1 separated the rainy season months (left side of the graph) from those of the dry season (right side). This was confirmed by the association of the swell vector with axis 1, as the swell is enhanced during the dry season due to reinforcement of the trade winds.

Long-Term Variations

To better understand the annual temporal variations of the herbivorous fish assemblages, two data sets were considered separately, the juveniles (< 5 cm) and the fish larger than 5 cm. The RDA ordinations of the sites measured monthly showed that the temporal distribution of the herbivore assemblage was cyclical, both in number of individuals and in biomass for the juveniles but only in number of individuals for the adults; lines are drawn in Figure 4 that follow the sampling time sequence. Results concerning the adult biomass were less clear because of the high variation of biomass from one species to another.

For numbers of adult individuals (Figure 4a), two PCNM variables (3 and 4) were significant ($p = 0.011$ and $p = 0.015$, respectively); they accounted together for 35.6% of the species temporal variance. The first canonical axis represented 34.8% of the variance and had a period of approximately 9 months (Figure 5a). The species contributing in an important way to the variation along this axis were *Sc. iserti* and *A. chirurgus*. The variance explained by axis 2 was very small, 0.86%.

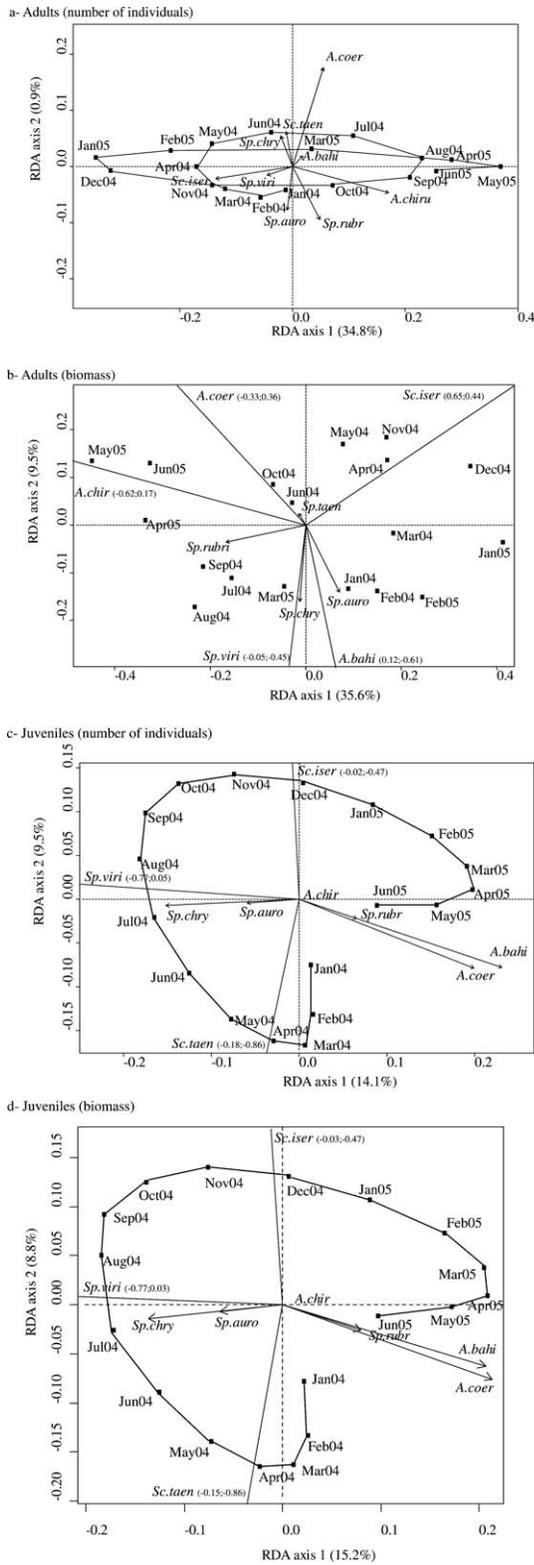


Figure 4. Correlation biplots based on RDA ordinations of the herbivorous fish species (*A.bahi* = *Acanthurus bahianus*, *A.chir* = *Acanthurus chirurgus*, *A.coer* = *Acanthurus coeruleus*, *O.atla* = *Ophioblennius atlanticus*, *Sc.iser* = *Scarus iserti*, *Sc.taen* = *Scarus taeniopterus*, *Sc.vetu*

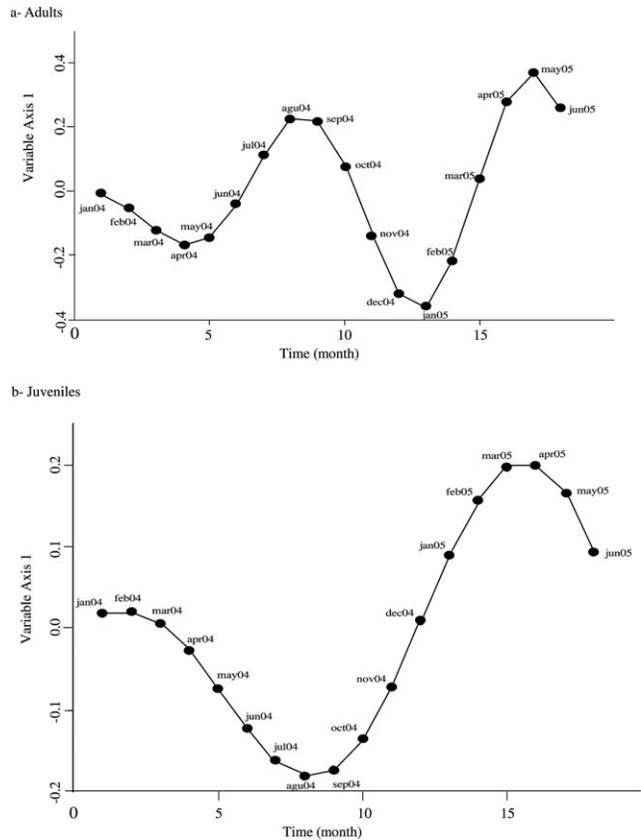


Figure 5. First canonical axis values of the PCNM analysis of (a) multispecies adults herbivorous fish and (b) multispecies juveniles, drawn as a function of time (abscissa). The analysis in (a) involved PCNMs 3 and 4 as explanatory variables and in (b) PCNMs 1 and 2.

Figure 4b revealed that three PCNM variables (3, 4, and 5) were significant ($p = 0.004$, $p = 0.020$, and $p = 0.032$, respectively) for the adult biomass; they explained 47.8% of the species temporal variance. The first canonical axis represented 35.6% of the variance and had a period of nine months, like for the numbers of adult individuals (Figure 5a). *Sc. iserti* and *A. chirurgus* were the species contributing the most to axis 1. Results concerning juvenile fish species are represented in Figure 4c and 4d. Two PCNM variables (1 and 2) were marginally significant for the number of juveniles ($p = 0.056$ and $p = 0.048$, respectively); they explained together 23.6% of the species temporal variance. The R^2 of the first canonical axis was 14.1%; that axis had a period of approximately 13 months (Figure 5b). This period was the same again

←
 = *Scarus vetula*, *Sp.auro* = *Sparisoma aurofrenatum*, *Sp.chry* = *Sparisoma chrysopterus*, *Sp.rubr* = *Sparisoma rubripinne*, *Sp.viri* = *Sparisoma viride*) constrained by the sampling months (■). The percentage reported along each axis refers to the percentage of the total variation in the herbivorous fish assemblage, which is accounted for by the canonical axis. Some species arrows end outside the graphs; the coordinates of their end points are given.

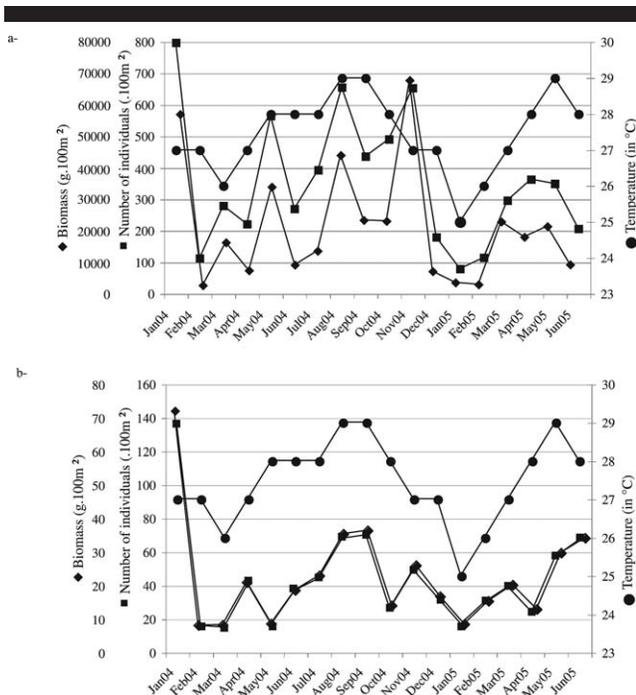


Figure 6. Relationship between fish counts (number.100 m⁻²) and biomass (g.100 m⁻²) for adults (a) and juveniles (b) on the one hand and water temperature (in °C) on the other hand.

for juvenile biomass. The R^2 of the first canonical axis was 15.2%, and the two significant PCNM variables (1 and 2) explained 24.0% of the species temporal variance. For both biomass and number of individuals, the species contributing the most to the variation along axis 1 were *Sp. viride* and *A. bahianus*.

Figure 6 shows the good relationship between fish densities (in number and biomass) and seawater temperature. As a season indicator, temperature is a good proxy for other variables, such as precipitation, wind, and swell, which dominate the yearly environmental variation in the Caribbean. The relationship is not linear because of the high fish count and biomass values observed in January 2004; this was due to the observation of a school of surgeonfish (Acanthuridae) which crossed the transect during the survey. However, Kendall rank correlations of water temperature with juvenile and adult counts and juvenile biomass were significant (juvenile counts: tau = 0.402, $p = 0.032$; adult counts: tau = 0.408, $p = 0.029$; juvenile biomass: tau = 0.393, $p = 0.023$) and very nearly significant for adult biomass (tau = 0.363, $p = 0.052$). Without the first month of observations, all correlations with temperature were significant (juvenile counts: tau = 0.499, $p = 0.010$; adult counts: tau = 0.506, $p = 0.009$; juvenile biomass: tau = 0.489, $p = 0.006$; adult biomass: tau = 0.456, $p = 0.018$). Results for both adults and biomass showed that herbivorous fish abundances were the lowest during the winter (December–February), whereas the maximum abundances were observed during the rainy season for juveniles and adults, with two peaks for adults in August and November.

DISCUSSION

This work was designed to examine spatial and temporal variations in the structure of herbivorous fish assemblages in some Caribbean coral reefs at several different scales. Significant variations were found among sites located around the island of Guadeloupe. The observations suggest many possible causes of spatial variations. Concerning temporal variations, the structure of the herbivorous fish assemblages varied significantly daily and seasonally.

Spatial Distribution

An important aim for reef fish ecologist is to explain differences in habitat utilization patterns among reef-associated species (Johansen, Bellwood, and Fulton, 2008). The distribution patterns of fish are often shaped by the interaction between their physiological capacities and the physical attributes of the environment like temperature, salinity, or water motion (Bellwood and Wainwright, 2001). Fish spatial distributions on coral reefs were reviewed in detail by Williams (1991). Food availability, coral reef complexity, presence of shelter, and benthic cover, as well as dispersal, settlement, competition, and predation, are thought to be determinants of habitat use in reef fishes. Wave exposure was also identified as a factor determining reef fish distribution. However, the ability of each species to cope with the biophysical characteristics of the local environment must also set overall limits to the range of potential habitats that can be occupied (Johansen, Bellwood, and Fulton, 2008). For herbivorous fishes, the greatest source of variations in community structure is seen at the habitat or reef-zone scale (Russ, 1984). Physical factors determine the cross-shelf patterns, with incident wave action being the main physical factor accounting for differences in fish communities among habitats (Russ, 1984; Williams, 1982).

During the present study, the considered factors were depth, benthic cover, and protection status. The results highlighted the importance of depth for the distribution of herbivorous fish, with a strong difference between the herbivorous assemblage on reefs flats and that on reef slopes. While the maximal densities of herbivorous fish were found on reef flats, their biomass was higher on reef slopes, where the fish were larger. Indeed, reefs flats are the habitat of predilection for herbivorous juveniles, where they are numerous but with small biomass (Bouchon-Navaro and Harmelin-Vivien, 1981; Robertson, Polunin, and Leighton, 1979; Sale, 1969). The densities in the present study are high for the Caribbean (Lewis, 1986; Lewis and Wainwright, 1985; van Rooij, Videler, and Bruggemann, 1998; Williams and Polunin, 2001) and are closer to those of the Indo-Pacific (Gust, Choat, and McCormick, 2001; Harmelin-Vivien, 1984; Robertson, Polunin, and Leighton, 1979). Concerning biomass, the values obtained in Australia (Gust, Choat, and McCormick, 2001) and in Bonaire (Bruggemann, van Oppen, and Breeman, 1994; van Rooij, Videler, and Bruggemann, 1998) are higher than in Guadeloupe.

Acanthuridae were more abundant on reef flats, whereas Scaridae predominated on reef slopes. This difference in dominance has been noted by Lewis and Wainwright (1985) on the coral reefs of Belize; Acanthuridae were abundant in

shallow waters above a 5-m depth, while Scaridae were abundant deeper. Bouchon-Navaro and Harmelin-Vivien (1981) also observed this separation between the two herbivorous families according to depth in the Red Sea. They showed that in Aqaba surgeonfish (Acanthuridae) dominate the reef flat and parrotfish (Scaridae) the outer slope. In contrast, at Aldabra Atoll in the Indian Ocean, Robertson, Polunin, and Leighton (1979) found parrotfish to be more abundant on the reef crest and surgeonfish on deeper reef slopes. In the same way, in Takapoto (French Polynesia), Acanthuridae dominated the reef slopes and Scaridae the shallower areas (Bouchon-Navaro, 1983).

Several explanations for the observed changes in species composition with depth are possible. To explain this different habitat use, Bellwood and Wainwright (2001) hypothesized that there was a strong correlation between estimated swimming performance and degree of water movement. They suggested that swimming performance in fishes limits access to high-energy locations and may be a significant factor influencing habitat use. The difference in Scarid or Acanthurid dominance between reef slopes and reef flats may be directly linked to the functional attributes of fish species and particularly to their swimming performance (Fulton and Bellwood, 2005; Fulton, Bellwood, and Wainwright, 2005). Exposed shallow habitats (like reef flats) displayed the highest flow velocities with the value decreasing with increasing depth. Consequently, the fast swimmers would be the most abundant in high-energy locations, where they encounter high hydrodynamic action, and slower swimmers would be most abundant in sheltered locations.

Another explanation may be the nutritional ecology of herbivorous fish. Indeed, grazers may detect small changes in algal nutritional value (Zemke-White, Choat, and Clements, 2002) and with increasing depth, the lower levels of irradiance alter the nutritional values of algae. It is so possible that herbivores distribute themselves accordingly. Irradiance may also have an effect on algal palatability. According to Cronin and Hay (1996), high levels of ultraviolet light found in shallow waters decrease the abundance of some secondary metabolites and thus make shallow algae more susceptible to grazing.

Temporal Variation

The present study has shown the existence of temporal variation in the herbivorous fish assemblage of the reef flats. Some are short termed: the fish leave the reef flat at low tide and when a choppy sea is settled. Other variations are seasonal. The largest numbers of individuals and biomass were observed during the rainy season and the minimal abundances between December and February in the dry season.

Another study in coral reef of Guadeloupe (Bouchon-Navaro, 1997) showed that herbivorous fish presented an annual cycle, with the maximum number of individuals observed in the rainy season (May–September) and the minimum during the dry season (November–April). However, some authors did not find seasonality in the herbivore assemblage (Duffy and Hay, 1990). In tropical areas, they noticed that herbivores are abundant and active all year long. They argued that seasonality is found

on temperate systems and that herbivorous fish are more active during the summer. In Australia, Booth (1998) also noted that herbivorous scarid abundances were not influenced by seasons.

The present study showed that juvenile herbivores presented peaks of abundance between June and September. In their studies in Curaçao and Guadeloupe, Luckhurst and Luckhurst (1977) and Bouchon-Navaro (1997), respectively, had identified juvenile peaks of abundance between May and July and then between September and November.

Water temperature was identified as an important factor structuring the temporal variations of adult and juvenile herbivores. According to Munro (1983), the presence of coral reef fish larvae in the plankton is linked to water temperature, larvae being rare when water temperature is higher than 28°C, and the maximum abundance of fish larvae may be observed in February, March, and April in Caribbean waters. In the present study, water temperature did not exceed 28°C during these months. Reeson (1983a, 1983b) also suggested that the period of reproduction for Acanthuridae and Scaridae is between January and March. For Randall and Randall (1963), this privileged period is linked to water temperature, which is colder during that season. As herbivores have a pelagic larval phase between 50 and 70 days (Rocha *et al.*, 2002; Thresher, 1984), which may explain the high abundance of juveniles observed on the reefs between June and September.

Besides the arrival of juveniles during the rainy season, another hypothesis was formulated to explain the higher fish abundances during this period (Letourneur 1996b; Letourneur *et al.*, 2008) to explain the higher fish abundances during this period. He argued that during this period reef flats are used for habitat and food resources by fish usually avoiding it during the dry season, when wave action is severe. For this author, the latter explanation mainly concerned schooling herbivores such as parrotfish and surgeonfish. This hypothesis may explain the results of the present study: the swell was indeed the highest during December, January, and February, when the lowest herbivore abundances were observed.

CONCLUSIONS

The present work provided new descriptive information on the structure in space and time of herbivorous fish assemblages in the French West Indies. We demonstrated that the herbivorous fish assemblage is highly shaped by the coral reefs environmental factors. In light of the global coral reef crisis, the contribution of each of these factors needs to be among the main goals of future research on herbivorous coral reef fishes. Indeed, our ability to detect responses of herbivorous fish assemblages to spatial and temporal variables can lead to some more adapted management measures and to more effective means of reducing ecosystem disturbance.

ACKNOWLEDGMENTS

The authors express their thanks to the Réserve Marine du Grand Cul-de-Sac Marin for their authorization to work in the protected areas.

LITERATURE CITED

- Bellwood, D.R. and Alcalá, A.C., 1988. The effect of a minimum length specification on visual estimates of density and biomass of coral reef fishes. *Coral Reefs*, 7, 23–27.
- Bellwood, D.R. and Choat, J.H., 1989. A description of the juvenile phase colour patterns of 24 parrotfish species (family Scaridae) from the Great Barrier Reef, Australia. *Records of the Australian Museum*, 41, 1–41.
- Bellwood, D.R. and Wainwright, P.C., 2001. Locomotion in labrid fishes: implications for habitat use and cross-shelf biogeography on the Great Barrier Reef. *Coral Reefs*, 20, 139–150.
- Bohnsack, J.E. and Harper, D.E., 1988. Length–weight relationships of selected marine reef fishes from Southern United States and the Caribbean. NOAA Technical Memorandum NMFS-SEFC-215, 31p.
- Booth, D.J., 1998. Grazing pressure of roving and territorial fishes on patch reef in One Tree Lagoon. In: Greenwood, J.G. and Hall, N.J. (eds.), *Proceedings of the Australian Coral Reef Society 75th Anniversary Conference*. Brisbane, Australia: School of Marine Science, University of Queensland, pp. 15–27.
- Borcard, D. and Legendre, P., 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling*, 153, 51–68.
- Bouchon, C.; Portillo, P.; Bouchon-Navarro, Y.; Louis, M.; Hoetjes, P.; Brathwaite, A.; Roach, R.; Oxenford, H.; O'Farrell, S., and Day, O., 2008. Status of coral reefs in the Lesser Antilles after the 2005 coral bleaching event. In: Wilkinson, C. and Souter, D. (eds.), *Status of Caribbean Coral Reefs after Bleaching and Hurricanes in 2005*. Townsville: Global Coral Reef Monitoring Network and Reef and Rainforest Research Center, pp. 85–104.
- Bouchon-Navarro, Y., 1983. Distribution quantitative des principaux poissons herbivores (Acanthuridae et Scaridae) de l'atoll de Takapoto (Polynésie française). *Journal de la Société des Océanistes*, 77, 43–54 [in French].
- Bouchon-Navarro, Y., 1997. Les Peuplements Ichtyologiques Récifaux des Antilles: Distribution Spatiale et Dynamique Temporelle. Guadeloupe, France: University of the French West Indies, Ph.D. thesis, 242p [in French].
- Bouchon-Navarro, Y. and Harmelin-Vivien, M.L., 1981. Quantitative distribution of herbivorous reef fishes in the Gulf of Aqaba (Red Sea). *Marine Biology*, 63, 79–86.
- Bruggemann, J.H.; van Oppen, M.J.H., and Breeman, A.M., 1994. Foraging by the stoplight parrotfish *Sparisoma viride*. I. Food selection in different, socially determined habitats. *Marine Ecology Progress Series*, 106, 41–55.
- Claro, R. and García-Arteaga, J.P., 1994. Crecimiento. In: Claro, R. (ed.), *Ecología de los Peces Marinos de Cuba*. Chetumal, Mexico: Centro de Investigaciones de Quintana Roo, pp. 321–402.
- Cronin, G. and Hay, M.E., 1996. Susceptibility to herbivores depends on recent history of both the plant and animal. *Ecology*, 77, 1531–1543.
- Dray, S.; Legendre, P., Peres-Neto, P., 2006. Spatial modeling: a comprehensive framework for principal coordinate analysis of neighbor matrices (PCNM). *Ecological Modelling*, 196, 483–493.
- Dray, S., 2005. Packfor: forward selection with multivariate Y by permutation under reduced model. Laboratoire Biométrie et Biologie Évolutive, Lyon. Available at: <http://biomserv.univ-lyon1.fr/~dray/software.php>.
- Duffy, J.E. and Hay, M.E., 1990. Seaweed adaptations to herbivory. *Bioscience*, 40, 368–375.
- Fulton, C.J. and Bellwood, D.R., 2005. Wave-induced water motion and the functional implications for coral reef fish assemblages. *Limnology and Oceanography*, 50, 255–264.
- Fulton, C.J.; Bellwood, D.R., and Wainwright, P.C., 2005. Wave energy and swimming performance shape coral reef fish assemblages. *Proceedings of the Royal Society Biological Sciences*, 272, 827–832.
- Galzin, R., 1987a. Structure of fish communities of French Polynesian coral reefs. I. Spatial scales. *Marine Ecology Progress Series*, 41, 129–136.
- Galzin, R., 1987b. Structure of fish communities of French Polynesian coral reefs. II. Temporal scales. *Marine Ecology Progress Series*, 41, 137–145.
- Gardner, T.A.; Côté, I.M.; Gill, J.A.; Grant, A., and Watkinson, A.R., 2003. Long-term region-wide declines on Caribbean corals. *Science*, 301, 958–960.
- Guadeloupe National Park. (2005). Welcome to the Official Site. <http://www.guadeloupe-parcnational.com> (accessed January 2006).
- Gust, N.; Choat, J.H., and McCormick, M.I., 2001. Spatial variability in reef fish distribution, abundance, size and biomass: a multi-scale analysis. *Marine Ecology Progress Series*, 214, 237–251.
- Harmelin-Vivien, M.L., 1984. Distribution quantitative des poissons herbivores dans les formations coralliennes. ORSTOM Tahiti. *Notes et Documents Océanographiques*, 22, 81–107 [in French].
- Hughes, T.P., 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, 265, 1547–1551.
- Hughes, T.P.; Baird, A.H.; Bellwood, D.R.; Card, M.; Connolly, S.R.; Folke, C.; Grosberg, R.; Hoegh-Guldberg, O.; Jackson, J.B.C.; Kleypas, J.; Lough, J.M.; Marshall, P.; Nyström, M.; Palumbi, S.R.; Pandolfi, J.M.; Rosen, B., and Roughgarden, J., 2003. Climate change, human impacts, and the resilience of coral reefs. *Science*, 301, 929–933.
- Hughes, T.P.; Bellwood, D.R.; Folke, C.S.; McCook, L.J., and Pandolfi, J.M., 2007a. No-take areas, herbivory and coral reef resilience. *Trends in Ecology and Evolution*, 22, 1–3.
- Hughes, T.P.; Rodriguez, M.J.; Bellwood, D.R.; Ceccarelli, D.; Hoegh-Guldberg, O.; McCook, L.; Moltschanivskiy, N.; Pratchett, M.S.; Steneck, R.S., and Willis, B., 2007b. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology*, 17, 1–6.
- Jackson, J.B.C.; Kirby, M.X.; Berger, W.H.; Bjorndal, K.A.; Botsford, L.W.; Bourque, B.J.; Bradbury, R.H.; Cooke, R.G.; Erlanson, J.; Estes, J.A.; Hughes, T.P.; Kidwell, S.M.; Lange, C.B.; Lenihan, H.S.; Pandolfi, J.M.; Peterson, C.H.; Steneck, R.S.; Tegner, M.J., and Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293, 629–638.
- Johansen, J.L.; Bellwood, D.R., and Fulton, C.J., 2008. Coral reef fishes exploit flow refuges in high-flow habitats. *Marine Ecology Progress Series*, 360, 219–226.
- Kopp, D., 2007. Les Poissons Herbivores dans l'Écosystème Récifal des Antilles. Guadeloupe, France: University of the French West Indies, Ph.D. thesis, 198p [in French].
- Lapointe, B.E., 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. *Limnology and Oceanography*, 42, 1119–1131.
- Legendre, P. and Durand, S., 2009. Canonical redundancy analysis (RDA test). Electronic references. Montréal, Québec, Canada: Département des Sciences Biologiques, Université de Montréal.
- Legendre, P. and Birks, H.J.B., 2010. From classical to canonical ordination. In: Birks, H.J.B.; Lotter, A.F.; Juggins, S., and Smol, J.P. (eds.), *Tracking Environmental Change using Lake Sediments. Volume 5: Data Handling and Numerical Techniques*. Dordrecht: Springer.
- Legendre, P. and Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia*, 129, 271–280.
- Legendre, P. and Legendre, L., 1998. *Numerical Ecology*, 2nd English ed. Amsterdam: Elsevier Science BV, 853p.
- Letourneur, Y., 1996a. Dynamics of fish communities on Reunion fringing reefs, Indian Ocean. I. Patterns of spatial distribution. *Journal of Experimental Marine Biology and Ecology*, 195, 1–30.
- Letourneur, Y., 1996b. Dynamics of fish communities on Reunion fringing reefs, Indian Ocean. II. Patterns of temporal fluctuations. *Journal of Experimental Marine Biology and Ecology*, 195, 31–52.
- Letourneur, Y.; Gaertner, J.-C.; Durbec, J.-P., and Jessus, M.E., 2008. Effects of geomorphological zones, reefs and seasons on coral reef fish communities of Réunion Island, Mascarene Archipelago, SW Indian Ocean. *Estuarine Coastal and Shelf Science*, 77, 697–709.
- Lewis, S.M., 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecological Monographs*, 56, 183–200.
- Lewis, S.M. and Wainwright, P.C., 1985. Herbivore abundance and grazing intensity on a Caribbean coral reef. *Journal of Experimental Marine Biology and Ecology*, 87, 215–228.

- Lucas, H.A. and Seber, G.A.F., 1977. Estimating coverage and particle density using the line intercept method. *Biometrika*, 64, 618–622.
- Luckhurst, B.E. and Luckhurst, K., 1977. Recruitment patterns of coral reef fishes on the fringing reef of Curaçao, Netherlands Antilles. *Canadian Journal of Zoology*, 55, 681–689.
- McClanahan, T.R.; Steneck, R.S.; Pietri, D.; Cokos, B.A., and Jones, S., 2005. Interaction between inorganic nutrients and organic matter in controlling coral reef communities in Glovers Reef Belize. *Marine Pollution Bulletin*, 50, 566–575.
- Mumby, P.J.; Dahlgren, C.P.; Harborne, A.R.; Kappel, C.V.; Micheli, F.; Brumbaugh, D.R.; Holmes, K.E.; Mendes, J.M.; Broad, K.; Sanchirica, J.N.; Buch, K.; Box, S.; Stoffle, R.W., and Gill, A.B., 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science*, 311, 98–101.
- Munday, P.L., 2004. Habitat loss, resource specialization, and extinction on coral reefs. *Global Change Biology*, 10, 1642–1647.
- Munro, J.L., 1983. Caribbean Coral Reef Fishery Resources: The Biology, Ecology, Exploitation and Management of Caribbean Reef Fishes. Scientific Report of the ODA/UWI Fisheries Ecology Research Project 1969–1973, ICLARM Studies Rev. 7. Jamaica: University of the West Indies, 276p.
- Paddock, M.J.; Cowen, R.K., and Sponaugle, S., 2006. Grazing pressure of herbivorous coral reef fishes on low coral-cover reefs. *Coral Reefs*, 25, 461–472.
- Pandolfi, J.M.; Bradbury, R.H.; Sala, E.; Hughes, T.P.; Bjorndal, K.A.; Cooke, R.G.; McArdle, D.; McClenachan, L.; Newman, M.J.H.; Paredes, G.; Warner, R.R., and Jackson, J.B.C., 2003. Global trajectories of the long-term decline of coral reef ecosystems. *Science*, 301, 955–958.
- Randall, J.E. and Randall, H.A., 1963. The spawning and early development of the Atlantic parrot fish, *Sparisoma rubripinne*, with notes on other scarid and labrid fishes. *Zoologica*, 48, 49–60.
- Rao, C., 1964. The use and interpretation of principal components analysis in applied research. *Sankhya Series*, A26, 329–358.
- Reeson, P.H., 1983a. The biology, ecology and bionomics of the parrotfishes, Scaridae. In: Munro, J.L. (ed.), Caribbean Coral Reef Fishery Resources: The Biology, Ecology, Exploitation and Management of Caribbean Reef Fishes. Scientific Report of the ODA/UWI Fisheries Ecology Research Project 1969–1973, ICLARM Studies Rev. 7. Jamaica: University of the West Indies, pp. 166–177.
- Reeson, P.H., 1983b. The biology, ecology and bionomics of the surgeonfishes, Acanthuridae. In: Munro, J.L. (ed.), Caribbean Coral Reef Fishery Resources: The Biology, Ecology, Exploitation and Management of Caribbean Reef Fishes. Scientific Report of the ODA/UWI Fisheries Ecology Research Project 1969–1973, ICLARM Studies Rev. 7. Jamaica: University of the West Indies, pp. 178–190.
- Robertson, D.R., 1988. Abundances of surgeonfishes on patch-reefs in Caribbean Panama: due to settlement, or post settlement events? *Marine Biology*, 97, 495–501.
- Robertson, D.R.; Polunin, N.V.C., and Leighton, K., 1979. The behavioral ecology of three Indian Ocean surgeonfishes (*Acanthurus lineatus*, *A. leucosternon* and *Zebrasoma scopas*): their feeding strategies, and social and mating systems. *Environmental Biology of Fishes*, 4, 125–170.
- Rocha, L.A.; Bass, A.L.; Robertson, R., and Bowen, B.W., 2002. Adult habitat preferences, larval dispersal, and the comparative phylogeography of three Atlantic surgeonfishes (Teleostei: Acanthuridae). *Molecular Ecology*, 11, 243–252.
- Russ, G.R., 1984. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. *Marine Ecology Progress Series*, 20, 23–34.
- Sale, P.F., 1969. Pertinent stimuli for habitat selection by the juvenile manini. *Ecology*, 50, 616–623.
- Service Hydrologique et Océanographique de la Marine. 2010. Service Hydrologique et Océanographique de la Marine. <http://www.shom.fr> (accessed July 2005).
- ter Braak, C.J.F., 1990. *Updates Notes: CANOCO* (v. 3.10). Wageningen, the Netherlands: Agricultural Mathematics Group.
- ter Braak, C.J.F. and Šmilauer, P., 2002. *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination* (v. 4.5). Ithaca, New York: Microcomputer Power.
- Thresher, R.E., 1984. *Reproduction in Reef Fishes*. Neptune City, New Jersey: T.F.H. Publications, 399p.
- van Rooij, J.M.; Videler, J.J., and Bruggemann, J.H., 1998. High biomass and production but low energy transfer efficiency of Caribbean parrotfish: implications for trophic models of coral reefs. *Journal of Fish Biology*, 53, 154–178.
- Wilkinson, C. and Souter, D., 2008. *Status of Caribbean Coral Reefs after Bleaching and Hurricanes in 2005*. Townsville, Australia: Global Coral Reef Monitoring Network and Reef and Rainforest Research Center, 150p.
- Williams, D.Mc.B., 1982. Patterns in the distribution of fish communities across the central Great Barrier Reef. *Coral Reef*, 1, 35–43.
- Williams, D.Mc.B., 1983. Daily, monthly and yearly variability in recruitment of a guild of coral reef fishes. *Marine Ecology Progress Series*, 10, 231–237.
- Williams, D.Mc.B., 1991. Patterns and processes in the distribution of coral reef fishes. In: Sale, P. (ed.), *The Ecology of Fishes on Coral Reefs*. San Diego, California: Academic Press, pp. 437–474.
- Williams, I.D. and Polunin, N.V.C., 2001. Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. *Coral Reefs*, 19, 358–366.
- Zemke-White, W.L.; Choat, J.H., and Clements, K.D., 2002. A re-evaluation of the diel feeding hypothesis for marine herbivorous fishes. *Marine Biology*, 141, 571–579.