Diversity of Trophic Niches among Scaridae (Guadeloupe, Lesser Antilles)

Diversidad de los Nichos Tróficos entre los Scaridae (Guadeloupe, Antillas Menores)

Diversité des Niches Trophiques Parmi les Scaridae (Guadeloupe, Lesser Antilles)

CHARLOTTE DROMARD[1]*, YOLANDE BOUCHON-NAVARO[1],
MIREILLE HARMELIN-VIVIEN[2], and CLAUDE BOUCHON[1]
[1]*DYNECAR, Université des Antilles et de la Guyane, Laboratoire de Biologie Marine, Campus de Fouillole Pointe-à-Pitre, Guadeloupe 97159 France. *cdromard@univ-ag.fr.* [2]*Mediterranean Institute of Oceanography, Aix-Marseille University Campus de Luminy, Case 901 Marseille 13288 France.*

ABSTRACT

Scaridae (parrotfishes) represent a common family of herbivorous fishes on Caribbean reefs. They play a major role in controlling the algal dynamics of the reef benthic communities and are widely exploited by Caribbean fisheries. In this study, we stated the hypothesis that the coexistence of different species of Scaridae is allowed by the diversity of their trophic niches. To investigate this fact, a study was conducted on seven species of Scaridae (*Sparisoma chrysopterum, S. rubripinne, S. aurofrenatum, S. viride, Scarus iseri, S. taeniopterus* and *S. vetula*), abundant on the reefs of Guadeloupe. Gut content analyses were coupled with stable isotope analyses ($^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios) to determine the trophic niche of the seven species. The contribution of sources to the fish diets was estimated using a mixing model. These fishes presented small $\delta^{15}N$ differences, whereas they showed more scattered $\delta^{13}C$ values, which imply the use of diversified sources of carbon. Among the seven studied species, three types of trophic niche were found. A first group of fishes, constituted by *Sparisoma chrysopterum*, *S. rubripinne* and *Scarus iseri,* mostly used macroalgae, especially algae at a juvenile stage present in the turf. *Sparisoma viride*, *Scarus vetula* and *S. taeniopterus* were grouped together due to their common use of living coral as protein intake along with macroalgae. Finally, *Sparisoma aurofrenatum* presented a specific diet, principally based on the assimilation of algal turf.

The seven scarids species ingest and assimilate differently the food items, presenting thus different trophic niches. This diversity could allow them to share food resources without competitive interactions.

KEY WORDS: Scaridae, Gut content analysis, stable isotope analysis, trophic niches, Caribbean reefs

INTRODUCTION

Parrotfishes (Scaridae) have been widely studied due to the major ecological role they play on coral reefs (Bellwood and Choat 1990, Mumby et al. 2006). Since the decline of the sea urchin *Diadema antillarum* (Lessios *et al*. 1984) which has led to the "coral-algal phase shift", herbivorous fishes have become the dominant grazers on Caribbean reefs (Carpenter 1990, Done 1992, Mumby et al. 2006). Moreover, Caribbean fisheries commonly exploit parrotfishes that represent a strong commercial interest (Mumby et al. 2006, Polunin and Robert 1993).

Previous studies on herbivorous fishes have led to divide parrotfishes into "functional groups", defined as a collection of species that perform a similar function, irrespective of their taxonomic affinities (Steneck and Dethier 1994). The description of functional groups is linked to the feeding behaviors of fishes, that is how they feed, what they consume, and their impact on the underlying substratum (Cardoso et al. 2009, Green and Bellwood 2009). Fishes from the genus *Sparisoma* are defined as "grazers", intensely grazing epilithic algal turf and detritus. Small *Scarus* species are considered as "scrapers", feeding principally on epilithic algal turf and removing some components of the reef substratum as they feed. Finally, large *Scarus* species differed from "scrapers" in the amount of substratum they remove and are cited as important "bioeroders". Even if parrotfishes are less diversified in the Caribbean (12 species) than in other regions of the world (67 species), their functional diversity has also been described in the Caribbean, giving important information on their ecological role (Bruggemann et al. 1994, 1996, Burkepile and Hay 2011, Froese and Pauly 2012, McAfee and Morgan 1996). However, description of their trophic niche with accuracy remains challenging.

The principal difficulty in describing the trophic niche of parrotfishes comes from their ability to grind the ingested food items into small fragments with their pharyngeal mill. Thus, few studies have identified the diet of parrotfishes based on direct observations of the gut contents (Randall 1967). Other authors described diets of parrotfishes by counting the "bites" during observations on the field (Burkepile and Hay 2008, Cardoso et al. 2009, Frydl and Stearn 1978, Kopp et al. 2010, McAfee and Morgan 1996). This method gives information on the feeding behavior but does not provide an accurate description of the diet. For example, direct observations on the field cannot quantify with precision the amount of food sources ingested.

More recently, stable isotope analyses have been proposed to reflect the diet of individuals over long periods, corresponding to the period during which the tissues of the consumers are synthetized (Bearhop et al. 2004). Thus, it has been argued that niche axes may be determined using stable isotope ratios (Bearhop et al. 2004) and have been formalized in the concept of the "isotopic niche" (Newsome et al. 2007) according to the fact that values measured in consumer tissues are linked to those of their diet with a constant enrichment at each trophic level (Minagawa and Wada 1984). Although isotopic

niche is likely to be tightly correlated to the trophic niche, these are not the same and should not be confused. Over the last two decades, a number of isotope mixing models have been proposed to identify the relative contributions of food resources to a consumer's diet (Layman et al. 2012). In this study, we used a concentration-dependant mixing model because of the presence of animal and vegetal items in diets (Phillips and Koch 2002). This model, performed with Stable Isotope Analysis with R (SIAR), is based on a series of related linear equations that utilize Bayesian statistics technics to identify proportional contributions of sources pools (Parnell et al. 2010).

Thus, while digestive contents gave a snapshot of the diet, stable isotope analyses draw the isotopic niche of an organism and give information on the long-term assimilations of sources. Coupling these two methods provides a powerful tool to determine the trophic niche of fish species. To our knowledge, these two approaches have never been used to describe trophic niches of parrotfishes.

In ecology, the coexistence of several species in a same habitat raises the question of the use of resources by different species. As parrotfishes share the same environment on reefs, the description of their trophic niche may be important to understand how they coexist without competitive interactions and which ecological role they specifically play on coral reefs.

The principal aim of the present study was to describe and compare the trophic niche of seven species of parrotfishes. To do so, we stated the hypothesis that the coexistence of parrotfishes can be explained by a difference of trophic niche among the seven species.

MATERIAL AND METHODS

Study Site and Field Samplings

This study was carried out in Guadeloupe, Lesser Antilles (16°30'N; 61°30'W). The studied site was located on the leeward side of the island and represented a surface of approximately 500 m x 100 m approximately (Figure 1). Maximum depth was 15 meters. The substratum was composed of rocky blocks colonized by a non reef-building coral community dominated by *Montastraea annularis* and *M. faveolata* coral species. Samples were collected along the studied site between September and November 2010. In this study, ten individuals of the seven parrotfishes were collected: *Sparisoma chrysopterum, S. rubripinne, S. aurofrenatum, S. viride, Scarus iseri, S. taeniopterus* and *S. vetula* (Table 1). Fish were immediately placed in an icebox to stop enzymatic activities and preserve gut and stomach contents. Mature erect macroalgae, called "macroalgae" in this study, were hand collected and preserved in a box. In addition, five replicates of algal turf, defined as a multi-specific assemblage of algae at a juvenile stage, mixed with small size species (Carpenter 1986, Hay 1981), were scraped and collected with an air sucker connected to a 500 µm meshed-collector bag. This method allowed us to sort benthic invertebrates from turf samples and to keep them as a potential food source. Finally, five pieces of live coral were sampled and kept on ice to preserve tissues. Coral samplings have been done on *Montastraea annularis*, because this species is the most abundant at the studied site and is often scraped by occasional coral-feeders in the Caribbean (Cole et al. 2008, Roff et al. 2011, Rotjan and Lewis 2008).

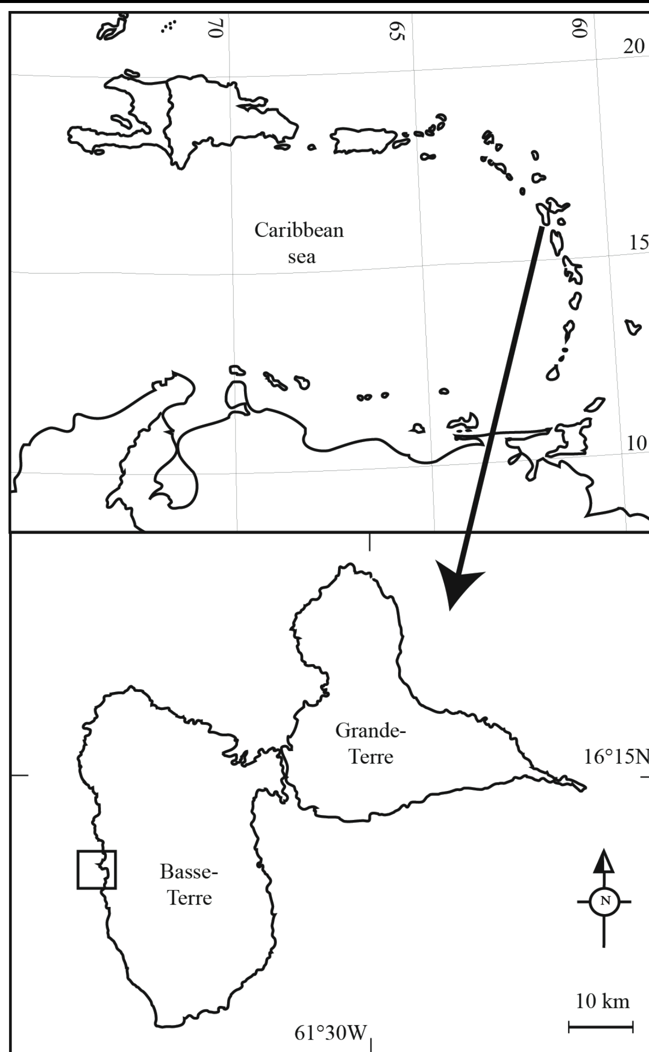

Figure 1. Location of the studied site in Guadeloupe.

Digestive Content Analysis

At the laboratory, total length of fish (L_T) was measured to the nearest millimeter. Wet body mass (M) was also noted to the nearest gram (Table 1). All individuals were speared at a maturity size (Froese and Pauly 2012). Fish were dissected and guts were placed in a 5% formaldehyde solution until analysis. Diets were determined by the method of point-intercept, originally described by Jones (1968). Gut contents were spread in a Petri dish and placed under a stereomicroscope. Ten points on each Petri dish were randomly chosen and photographed (10x magnification). A grid was superposed to the digitized

Table 1. Studied fish species, mean total length T_L in centimeter (range) and mean wet body mass M in gram (range) of fish. n_{DIET} is the number of samples used for digestive contents analyses and n_{ISO} is the number of sample used for isotopic analyses. Suggested functional groups are reported from the literature (Cardoso *et al*. 2009, Green and Bellwood 2009).

Fish species	n_{DIET}	n_{ISO}	T_L (cm)	M (g)	Functional groups
Scarus iseri	10	7	20.0 (18−22)	169 (99−225)	Scraper
Scarus taeniopterus	10	7	21.0 (19−25)	225 (137−367)	Scraper
Scarus vetula	10	7	26.0 (21−37)	389 (198−571)	Scraper/ Bioeroder
Sparisoma viride	10	7	27.0 (24−30)	373 (268−454)	Bioeroder
Sparisoma aurofrenatum	10	7	20.0 (19−21)	141 (119−156)	Grazer
Sparisoma chrysopterum	10	7	27.0 (23−32)	347 (202−543)	Grazer
Sparisoma rubripinne	10	7	20.0 (17−23)	177 (97−233)	Grazer

photographs and the nature of food items found under each point-intercept was recorded (Jones 1968). By this method, 1,000 points were reported per individual or 10,000 points per fish species. The results were then expressed as percentage of each food category ingested.

Stable Isotope Analysis

A small piece of the dorsal white muscle was cut on seven individuals of each fish species. Each sample of algal turf was sorted under a binocular microscope to exclude all benthic invertebrates that were preserved independently as a potential food source. The thallus of macroalgae was cleaned and scrapped to collect detritus, principally constituted by detrital organic deposits and bacteria (Crossman et al. 2001). Corals were scratched with a stainless steel blade to extrude polyps from the calcareous skeleton. All samples were cut into small pieces and oven dried at 50°C to a constant weight before being ground into an homogenous fine powder. Carbon and nitrogen stable isotope ratios of fish muscles and sources were determined on the same sample. Analyses were performed on two subsamples for food sources that might contain carbonates: calcified macroalgae, algal turf, detritus, invertebrates and corals. For $\delta^{13}C$, a subsample was acidified drop by drop with 1N HCl to remove calcified material that presents a less negative $\delta^{13}C$ than organic material (De Niro and Epstein 1978). For $\delta^{15}N$, a non-acidified subsample was used, as acidification can modify $\delta^{15}N$ (Pinnegar and Polunin 1999). Nitrogen and carbon isotope ratios were determined by a continuous flow mass spectrometer (Thermo Fisher™, delta V Advantage). Elemental concentrations of carbon and nitrogen ([C]% and [N]%) were measured with an elementary analyser (Thermo Fisher™, Flash EA 1112). Isotopic ratios were expressed in standard delta notation (δ values (‰)) according to the following formula: $\delta = (R_{sample}/R_{standard} - 1) \times 1000$, where R is the ratio of the heavy to light isotope (*i.e.* ^{15}N:^{14}N or ^{13}C:^{12}C), R_{sample} is measured for fish and sources and $R_{standard}$ is an international standard (Vienna Pee Dee belemnite limestone carbonate for carbon and atmospheric air for nitrogen).

The Bayesian mixing model SIAR v4.0 (Stable Isotope Analysis in R) developed by Parnell et al. (2010) was used to estimate the proportional contribution of food sources to the diet of fish species. As the elemental concentrations varied substantially among sources, the mixing model incorporated concentration dependence as recommended by Phillips and Koch (2002). This model deals with unequal assimilation of carbon and nitrogen, and assumes that for each element, the contribution of a source is proportional to the assimilated biomass times the elemental concentrations in that source. Three models were run according to each fish species. In each model, we entered the mean carbon and nitrogen signatures (± CI) of food sources and mean signatures of fish muscles, the mean elemental concentrations (± CI) of the sources ([C]% and [N]%) and carbon and nitrogen fractionation factors ($\Delta^{13}C$ and $\Delta^{15}N$). We fixed mean enrichments (± S.D.) of 1.5 ± 0.2‰ for the carbon and 4.5 ± 0.1‰ for the nitrogen, according to the data given in the previous literature (Sweeting et al. 2007, Mill et al. 2007, Wyatt et al. 2010).

Statistical Analysis

Data were tested for normality with the Shapiro-Wilks test and for homogeneity of variance with Levene's test. When all these assumptions were verified, we used analyses of variance (MANOVA and ANOVA) to compare the isotopic carbon and nitrogen signatures between food sources. Analyses of variance were combined with Tukey's honestly significant difference (HSD) post hoc tests to perform multiple comparisons. As data were not normal, isotopic signatures of fish muscle and the proportion of ingested food items were compared with Kruskal-Wallis tests. These tests were equally combined with post-hoc tests to perform multiple comparisons.

Contributions of food sources to fish diet (calculated with mixing models) have been compared between fish species with a Chi-square test. Finally, a hierarchical clustering (Bray-Curtis distance and method of Ward) was used to group fishes according to the proportions of sources they assimilated (calculated with mixing models) and the proportions of sources they ingested (measured with stomach content analysis). All statistical analyses were performed using the program R version 12.2.

RESULTS

Gut Content Analysis

Four categories of items were identified in stomach contents: calcified algae, algal turf, fleshy macroalgae and sediment (Figure 2). A large amount of unidentified material was observed in the digestive contents but was not regarded as a full-fledged type of source because of its uncertain origin. Unidentified material could represent ingested detritus, or result in the digestion on the other ingested sources as algae. Ingestion of sediment had been considered as incidental ingestion and resulting from the type of feeding. Considering the high proportion of unidentified material, it was difficult to statistically test the difference of diet between fish species. Among the four categories of food items, only two were differently ingested. The ingestion of sediment was significantly different according to fish species (Kruskal-Wallis, X^2 = 26.2, p = 0.0002) and *Scarus iseri* ingested the highest proportion of sediment. Proportions of calcified macroalgae ingested were equally different according to fish species (Kruskal-Wallis, X^2 = 24.3, p = 0.0004) and the gut contents of *Sparisoma aurofrenatum* showed the highest proportions of calcified macroalgae. To complete information on fish diets, the suggested functional group of each species were reported in Table 1.

Stable Isotope Analysis

Isotopic signatures of fish muscles and food sources were presented as a bi-plot in Figure 3. Among food sources, algal turf showed the lowest carbon signatures (mean ± CI = -19.0 ± 0.6‰) whereas the macroalgae *Acanthophora spicifera* presented the highest δ^{13}C (-14.6 ± 0.1‰). Benthic invertebrates displayed the highest δ^{15}N value, with a mean value (± CI) equal to 4.9 ± 1.1‰ and the macroalgae *Acanthophora spicifera* had the lowest nitrogen signatures (0.8 ± 0.1‰). Carbon and nitrogen signatures of food sources were significantly different from each other (MANOVA, Wilks' lambda = 0.01, $F_{7,32}$= 35.0, p < 0.0001). However, multiple comparison tests showed that *Dictyota* cf *pulchella* and *Acanthophora spicifera,* presented similar isotopic signatures of carbon and nitrogen (Tukey's HSD tests, both p > 0.99). Carbon signatures of the fish muscles were significantly different between fish species (Kruskal-Wallis, X^2 = 39.7, p < 0.0001). A significant difference was equally found between the nitrogen signatures of fish muscles (Kruskal-Wallis, X^2 = 37.6, p < 0.0001).

Mixing Models

To determine the contribution of food sources in the diet of each fish species, five potential sources were used in mixing models. Due to their close isotopic signatures,

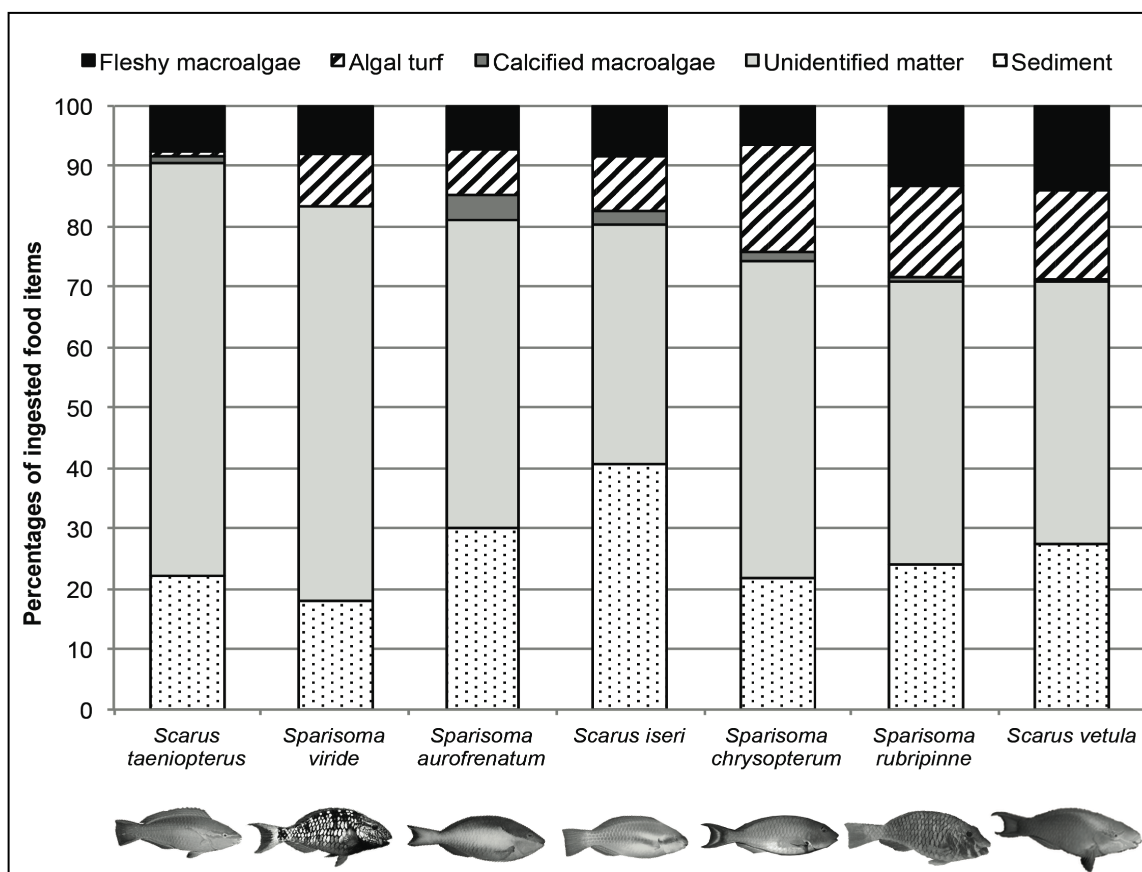

Figure 2. Proportions of ingested food categories (% of point-intercept) measured with gut contents analyses.

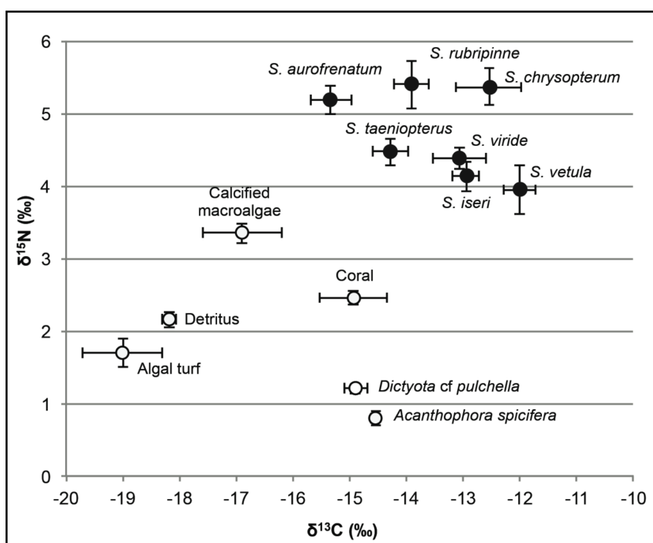

Figure 3. Mean isotopic signatures (± CI) of carbon ($\delta^{13}C$ ‰) and nitrogen ($\delta^{15}N$ ‰), measured in fish muscles and food sources collected on the reef. Calcified macroalgae: *Tricleocarpa fragilis* and *Amphiroa fragilissima*, Coral: *Montastraea annularis.*

the two macroalgae species *Dictyota* cf *pulchella* and *Acanthophora spicifera* were grouped in a same food category, called "fleshy algae". *Tricleocarpa fragilis* and *Amphiroa fragilissima* were grouped in a same food category "calcified algae". Algal turf and detritus were equally used as potential resource in the three models. Coral was only used as a potential source for three species known to feed on living coral: *Scarus vetula, S. taeniopterus* and *Sparisoma viride* (Cole et al. 2008, Roff et al. 2011, Rotjan and Lewis 2008). The elemental concentrations ([C]% et [N]%) and isotopic signatures of sources used in mixing models are presented in Table 2.

The contributions of food sources to the fish diet were significantly different between fish species (Chi-square test, $X^2 = 285.5$, d.f. = 24, $p < 0.001$; Table 3). According to the mean contributions of sources and the range of contributions (Bayesian 95% CI), fleshy macroalgae were preferentially assimilated by *Sparisoma chrysopterum*, *S. rubripinne* and *Scarus iseri* (Table 3). *Scarus vetula*, *S. taeniopterus* and *Sparisoma viride* assimilated mostly living coral and fleshy macroalgae while *S. aurofrenatum* principally assimilated algal turf.

Clustering Fishes According to Their Feeding Patterns

A hierarchical clustering was performed to group fish species according to the proportions of food sources they ingested and the proportions they assimilated (Figure 4). In this analysis, three groups of fish were identified. The first group of fish included *Sparisoma chrysopterum*, *S. rubripinne* and *Scarus iseri* that assimilated principally the fleshy macroalgae. A second group was constituted by the potential coral-feeders *Scarus vetula*, *S. taeniopterus* and *Sparisoma viride,* linked to the high proportions of coral they assimilated. Finally, a singleton appeared with *S. aurofrenatum*, who ingested the highest proportions of calcified macroalgae and assimilated the highest proportions of algal turf.

DISCUSSION

In this study, Caribbean parrotfishes were divided into three groups according to the type of trophic niche they occupy. Thus, a diversity of trophic niches was demonstrated among the seven studied species. While gut content analysis provided little information on the proportions of ingested food items, stable isotopes analyses allowed us to discriminate fish species according to the proportions of food sources they assimilate. The described trophic niches are occupied by one or several species, and the groups of fishes defined in this study differed from the suggested functional groups cited in the literature.

Sparisoma chrysopterum, *S. rubripinne* and *Scarus iseri* clustered in the same group, characterized by a high assimilation of fleshy macroalgae (> 50% of the total assimilation). The two first species were classified together in previous studies as "grazers" while S. iseri was described as a "scraper" (Cardoso et al. 2009). While the three species appeared to share a similar trophic niche, *S. iseri* slightly differed from *Sparisoma rubripinne* and *S. chrysopterum* by a higher proportion of ingested sediment.

Table 2. Mean ± CI $\delta^{13}C$ (‰), $\delta^{15}N$ (‰) and elemental concentrations ([C]% and [N]%) of food sources used in mixing models.
Fleshy macroalgae: *Dictyota* cf *pulchella* and *Acanthophora spicifera*;
Calcified macroalgae: *Tricleocarpa fragilis* and *Amphiroa fragilissima*.
Coral: *Montastraea annularis*.
n is the number of samples collected on the reef.

Sample types	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	[C]%	[N]%
Food sources					
Detritus	5	-18.2 ± 0.1	2.2 ± 0.1	6.8 ± 0.1	0.8 ± 0.02
Algal Turf	5	-19.0 ± 0.6	1.7 ± 0.2	7.6 ± 1.0	2.1 ± 0.5
Fleshy algae	6	-14.7 ± 0.2	1.0 ± 0.2	12.3 ± 3.0	1.9 ± 0.2
Calcified algae	9	-16.9 ± 0.7	3.4 ± 0.1	21.8 ± 3.6	8.8 ± 0.4
Coral	5	-14.9 ± 0.6	2.5 ± 0.1	44.8 ± 2.4	6.7 ± 1.2

Table 3. Mean (Bayesian 95% CI) biomass contribution of food sources to the diet of the seven species of Scaridae. Values in bold show important contributions.

Fish species	Detritus	Coral	Fleshy algae	Calcified algae	Algal turf
Sparisoma chrysopterum	14.4 (0.0−30.6)	–	72.9 (59.5−86.2)	1.7 (0.0−5.2)	11.0 (0.0−23.6)
Sparisoma rubripinne	8.4 (0.0−24.7)	–	83.9 (62.1−99.5)	1.1 (0.0−3.1)	6.6 (0.0−20.6)
Scarus iseri	6.0 (0.0−18.5)	–	87.6 (69.8−99.5)	1.9 (0.0−5.9)	4.5 (0.0−14.0)
Sparisoma aurofrenatum	26.1 (0.1−49.6)	5.1 (0.0−13.2)	22.9 (1.0−40.2)	9.0 (0.0−32.5)	36.9 (11.3−63.8)
Scarus taeniopterus	19.7 (0.0−38.7)	21.8 (2.7−37.6)	24.9 (0.1−48.6)	12.7 (0.0−30.9)	20.8 (0.4−38.9)
Scarus vetula	16.5 (0.0−35.9)	28.8 (1.4−51.9)	29.2 (0.1−57.2)	9.9 (0.0−27.9)	15.6 (0.0−34.7)
Sparisoma viride	13.5 (0.0−32.8)	31.8 (0.3−57.1)	35.9 (0.8−74.9)	6.9 (0.0−30.7)	11.9 (0.0−30.7)

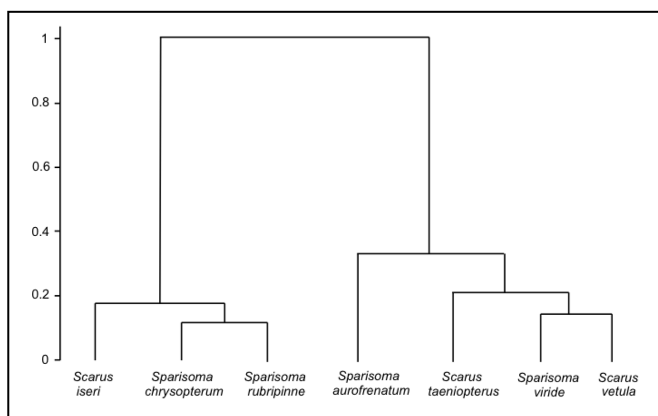

Figure 4. Hierarchical clustering of fish species according to the proportions of food items they ingested (measured with gut content analyses) and the proportions of food sources they assimilated (calculated with mixing models).

Generally, grazers and scrapers are known to avoid mature erect macroalgae, leading to incapacity to reverse a coral-algal phase-shift once it is established (Kopp et al. 2010, Mumby 2006). Thus, the important contribution of fleshy macroalgae could be linked to the consumption of macroalgae at a juvenile stage present in algal turf, which were excluded form turf samples during the preparation.

Sparisoma aurofrenatum is also classified as a grazer (Cardoso et al. 2009) and this assumption was verified in this study. Indeed, *S. aurofrenatum* principally assimilated algal turf and secondarily detritus. Fleshy macroalgae were also assimilated in a minor proportion while coral contributed slightly to its diet. In the clustering analysis, *S. aurofrenatum* occupied a specific trophic niche.

Finally, a third group of fishes was constituted by *Scarus vetula*, *S. taenopterus* and *Sparisoma viride*, in relation with the high contribution of living coral to their diet. While coral had not been identified as a main item in their diet (Hobson 1974, Randall 1967), these species were frequently observed feeding on live corals (Roff et al. 2011, Rotjan and Lewis 2005). In the present study, the results of mixing models indicated that living corals could represent high inputs of carbon and nitrogen to their diet, in complement to the contribution of fleshy macroalgae. These results support the fact that these three species, described as scrapers and bioeroders for the larger species (*Scarus vetula* and *Sparisoma viride*), have a greater eroding on the substratum than the other species, when foraging.

In conclusion, three types of trophic niche were described in this study, based on gut content and stable isotope analyses. Mixing models indicated different contribution of the food sources present on reefs to the diet of the seven parrotfishes. To our knowledge, this study is the first assessment of "long-term" assimilation of resources by parrotfishes in the Caribbean. This study highlighted the contribution of some food sources difficult to identify in gut contents, as detritus or corals tissue. Detritus have been described before as a potential resource for herbivorous fishes (Crossman et al. 2001, Wilson and Bellwood 1997) but few studies were carried out to quantify its contribution to fish diets. Even if the use of mixing models is widely open to debate (Fry 2013), the results of the present study gave new information on the diversity of trophic niche between Caribbean parrotfishes. The difference of trophic niche could explain the coexistence of the seven species in a same habitat without competitive interactions for food resources. These results also support the idea that species that share a similar trophic niche are redundant, while others seem to be complementary considering their ecological role on reefs (Burkepile and Hay 2011). Thus, the question of their conservation still appears to be primordial in the context of the coral-algal phase shift, especially because herbivorous fishes are often overfished in the Caribbean region (Mumby et al. 2006).

ACKNOWLEDGEMENTS

The authors express their thanks to P. Richard and G. Guillou, Université de la Rochelle - CNRS UMR LIENSs, for performing stable isotope analyses. We gratefully thank S. Cordonnier and L. Urvoix for their help in field samplings.

LITERATURE CITED

Bearhop, S., C.E. Adams, S. Waldrons, R.A. Fuller, and H. Macleod. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology* **73**:1007-1012.

Bellwood, D.R., and J.H. Choat. 1990. A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environmental Biology of Fishes* **28**:189-214.

Bruggemann, J.H., M.W.M., Kuyper, and A.M. Breeman. 1994. Comparative analysis of foraging and habitat use by the sympatric Caribbean parrotfish *Scarus vetula* and *Sparisoma viride* (Scaridae). *Marine Ecology Progress Series* **112**:51-66.

Bruggemann, J.H., A.M. van Kessel, J.M. van Rooij, and A.M. Breeman. 1996. Bioerosion and sediment ingestion by the Caribbean parrotfish *Scarus vetula* and *Sparisoma viride*: implication of fish size, feeding mode and habitat use. *Marine Ecology Progress Series* **134**:59-71.

Burkepile, D.E., and M.E. Hay. 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceeding of the National Academy of Sciences of USA* **105**:16201-16206.

Burkepile, D.E., and M.E. Hay. 2011. Feeding complementarity versus redundancy among herbivorous fishes on a Caribbean reef. *Coral Reefs* **30**:351-362.

Cardoso, S.C., M.C. Soares, H.A. Oxenford, and I.M. Côté. 2009. Interspecific differences in foraging behaviour and functional role of Caribbean parrotfish. *Marine Biodiversity Records* **2**:1-6.

Carpenter, R.C. 1986. Partitioning herbivory and its effects on coral reef algal communities. *Ecological Monographs* **56**:345-364.

Carpenter, R.C. 1990. Mass mortality of *Diadema antillarum* II: Effects on population densities and grazing intensity of parrotfishes and surgeonfishes. *Marine Biology* **104**:79-86.

Cole, A.J., M.S. Pratchett, and G.P. Jones. 2008. Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish and Fisheries* **9**:286-307.

Crossman, D.J., J.H. Choat, K.D. Clements, T. Hardy, and J. McConochie. 2001. Detritus as food for grazing fishes on coral reefs. *Limnology and Oceanography* **46**:1596-1605.

De Niro, M.J., and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* **42**:495-506.

Done, T.J. 1992. Phase-shifts in coral reefs communities and their ecological significance. *Hydrobiologia* **247**:121.

Froese, R., and D. Pauly. 2011. Fishbase. www.fishbase.org (accessed Jan 2012).

Fry, B. 2013. Alternative approaches for solving undetermined isotope mixing models. *Marine Ecology Progress Series* **472**:1-13.

Frydl, P., and C.W. Stearn. 1978. Rate of bioerosion by parrotfish in Barbados reef environments. *Journal of Sedimentary Petrology* **48**:1149-1158.

Green, A.L., and D.R. Bellwood. 2009. *Monitoring Functional Groups of Herbivorous Fishes as Indicators of Coral Reef Resilience-A Practical Guide for Coral Reef Managers in the Asia Pacific region*. IUCN working group on climate change and coral reefs. IUCN, Gland, Switzerland. 70 pp.

Hay, M.E. 1981. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. *Ecology* **62**:739-750.

Hobson, E.S. 1974. Feeding relationships of the teleostean fishes on coral reefs in Kona, Hawaii. *Fishery Bulletin* **72**:915-1031.

Jones, R.S. 1968. A suggested method for quantifying gut contents in herbivorous fishes. *Micronesica* **2**:369-371.

Kopp, D., Y. Bouchon-Navaro, S. Cordonnier, A. Haouisée, M. Louis, and C. Bouchon. 2010. Evaluation of algal regulation by herbivorous fishes on Caribbean coral reefs. *Helgoland Marine Research* **64**:181-190.

Layman, C.A., M.S. Araujo, R. Boucek, C.M. Hammerschlag-Peyer, E. Harrison, Z.R. Jud, P. Matich, A.E. Rosenblatt, J.J. Vaudo, L.A. Yeager, D.M. Post, and S. Bearhop. 2012. Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biological Research* **87**:545-562.

McAfee, S.T., and S.G. Morgan. 1996. Resource use by five sympatric parrotfishes in the San Blas Archipelago, Panama. *Marine Biology* **125**:427-437.

Mill, A.C., J.K. Pinnegar, and N.V.C Polunin. 2007. Explaining isotope trophic step fractionation: why herbivorous fish are different. *Functional Ecology* **21**:1137−1145

Minagawa, M., and E. Wada. 1984. Stepwise enrichment of 15N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. *Geochimica et Cosmochimica Acta* **48**:1135-1140.

Mumby, P.J. 2006. Phase shifts and the stability of macroalgae communities on Caribbean coral reefs. *Coral Reefs* **28**:761-773.

Mumby, P.J., C.P. Dahlgren, A.R. Harborne, C.V. Kappel, F. Micheli, D.R. Brumbaugh, K.E. Holmes, J.M. Mendes, K. Broad, J.N. Sanchirico, K. Buch, S. Box, R.W. Stoffle, and A.B. Gill. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* **311**:98-101.

Newsome, S.D., C. Martinez del Rio, S. Bearhop, and D.L. Phillips. 2007. A niche for isotopic ecology. *Frontiers in Ecology and the Environment* **5**:429-436.

Parnell, A.C., R. Inger, S. Bearhop, and A.L. Jackson. 2010. Source partitioning using stable isotopes: coping with too much variation. *PloS ONE* **5**:e9672.

Phillips, D.L., and P.L. Koch. 2002. Incorporating concentration dependence in stable isotope mixing models. *Oecologia* **130**:114-125.

Pinnegar, J.K., and N.V.C. Polunin. 1999. Differential fractionation of $\delta^{13}C$ and $\delta^{15}N$ among fish tissues: implication for the study of trophic interactions. *Functional Ecology* **13**:225-231.

Polunin, N.V.C., and C.M. Robert. 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Marine Ecology Progress Series* **100**:167−176.

Randall, J.E. 1967. Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography* **5**:665-847.

Roff, G., M.H. Ledlie, J.C. Ortiz, and P.J. Mumby. 2011. Spatial patterns of parrotfish corallivory in the Caribbean: the importance of coral taxa, density and size. *PLoS ONE* **6(12)**:e29133.

Rotjan, R.D., and S.M. Lewis. 2005. Selective predation by parrotfishes on the reef coral *Porites astreoides*. *Marine Ecology Progress Series* **305**:193-201.

Rotjan, R.D., and S.M. Lewis. 2008. Impact of coral predators on tropical reefs. *Marine Ecology Progress Series* **367**:73-91.

Steneck, R.S., and M.N. Dethier. 1994. A functional group approach to the structure of algal-dominated communities. *Oikos* **69**:476−498

Sweeting, C.J., J.T. Barry, N.V.C. Polunin, and S. Jennings. 2007. Effects of body size and environment on diet-tissue $\delta^{13}C$ fractionation in fishes. *Journal of Experimental Marine Biology and Ecology* **352**:165-176.

Wilson, S.K., and D.R. Bellwood. 1997. Cryptic dietary components of territorial damselfishes (Pomacentridae, Labroidei). *Marine Ecology Progress Series* **153**:299-310.

Wyatt, A.S.J., A.M. Waite, and S. Humphries. 2010. Variability in isotope discrimination factors in coral reef fishes: implications for diet and food web reconstruction. *PLoS ONE* **5(10)**:e13682.