

Gulf and Caribbean Research

Volume 28 | Issue 1

2017

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Recommended Citation

Dromard, C. R., Y. Bouchon-Navaro, M. Harmelin-Vivien and C. Bouchon. 2017. The nutritional quality of non-calcified macroalgae in Guadeloupe (Lesser Antilles) evaluated by their biochemical composition. *Gulf and Caribbean Research* 28 (1): GCF11-GCF16.

Retrieved from <https://aquila.usm.edu/gcr/vol28/iss1/6>

DOI: <https://doi.org/10.18785/gcr.2801.04>

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GULF AND CARIBBEAN

R E S E A R C H

Volume 28
2017
ISSN: 2572-1410



Published by

**THE UNIVERSITY OF
SOUTHERN MISSISSIPPI**

GULF COAST RESEARCH LABORATORY

Ocean Springs, Mississippi

GULF AND CARIBBEAN FISHERIES INSTITUTE PARTNERSHIP

THE NUTRITIONAL QUALITY OF NON-CALCIFIED MACROALGAE IN GUADELOUPE (LESSER ANTILLES) EVALUATED BY THEIR BIOCHEMICAL COMPOSITION

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KEY WORDS: Macronutrients, seaweed, food preferences, herbivorous fishes

INTRODUCTION

Climate change, marine pollution and overfishing on reef environments have led to an increasing colonization of macroalgae which compete with corals for space. This coral-algal phase shift is identified as a major threat for coral reefs (Hughes 1994). Cover and biomass of benthic macroalgae increase concurrently with coral loss, resulting in a shift from communities dominated by corals to communities dominated by macroalgae (Done 1992, McManus and Polsenberg 2004). This change has been attributed to an increasing input of nutrients in the ocean due to land-based pollution (agriculture, wastewater), a fragilization of the reef ecosystem due to climate changes (bleaching events, diseases) and the loss of major herbivorous organisms due to overfishing (Hughes 1994, McManus and Polsenberg 2004). Herbivorous fishes and urchins are key taxonomic groups to control and reverse this phenomenon (Bellwood et al. 2004, Ledlie et al. 2007). In the Caribbean, the principal herbivorous fishes are parrotfishes (Scaridae) and surgeonfishes (Acanthuridae). These groups are widely harvested and consumed in the whole region. Other herbivorous reef organisms are sea urchins, like *Diadema antillarum*. However, that species suffered from a massive mortality by epizootic disease between 1983 and 1984 (Lessios et al. 1984), leading to a severe depletion of their populations.

Herbivorous fishes and sea urchins principally consume early life stages of macroalgae, maintaining an algal turf on coral reefs (Lubchenco and Gaines 1981, Burkepile and Hay 2010). With a loss of grazing pressure, macroalgae reach mature forms which are difficult to remove when established. Mature forms of macroalgae are generally avoided by herbivorous organisms due to their morphological and physiological strategies against herbivory such as calcification or synthesis of repellent molecules (Lubchenco and Gaines 1981, Norris and Fenical 1982, Lewis 1985, Hay 1991).

Dietary behaviors of herbivorous fishes have been studied

for a long time due to their ecological role in the regulation of macroalgae (Ogden and Lobel 1978, Lewis 1985). Several studies were conducted to determine food preferences of herbivorous fishes with direct observations in the field (McAfee and Morgan 1996, Kopp et al. 2010), experiments of cage exclusion (Burkepile and Hay 2011), feeding preferences assays using transplant experiments (Lewis 1985, Paul and Hay 1986, Mantyka and Bellwood 2007), gut content analyses (Randall 1967) or stable isotopes analyses (Plass-Johnson et al. 2013, Dromard et al. 2015). Some macroalgae are unanimously cited as preferred species for herbivorous fishes, like *Acanthophora spicifera* (Littler et al. 1983, Lewis 1986, Paul and Hay 1986) or *Padina* (Ogden 1976, Lewis 1985, Paul and Hay 1986, Mantyka and Bellwood 2007). Some species are differently consumed according to site or the phyla. For example, *Laurencia* spp. seems to be widely consumed by herbivorous fishes in Australia (Mantyka and Bellwood 2007), while this species appears to be avoided by fishes in the Caribbean (Ogden 1976). In the Caribbean, *Laurencia* is a preferred macroalgae for the queen conch *Strombus gigas* (Lapointe et al. 2004). Finally some macroalgae genera, such as *Dictyota* spp. and *Caulerpa* spp., seem to be avoided by herbivorous fishes (Paul and Hay 1986).

Food preferences for herbivorous fishes can be explained by several factors, including algal structure, chemical defenses, and nutritional quality. It has been suggested that the probability of being eaten changes as a function of seaweed morphology. Indeed, filamentous algae and sheet-like algae are more likely to be consumed than calcareous macroalgae (Steneck and Watling 1982, Littler et al. 1983, Paul and Hay 1986, Hay 1991). Food choices can also be explained by the chemical defenses of macroalgae. Some species are able to synthesize repellent molecules, which deter herbivores and inhibit grazing by influencing their palatability (Paul and Hay 1986, Targett et al. 1986, Hay and Fenical 1988). Finally,

* This short communication is based on a presentation given in November 2016 at the 69th annual Gulf and Caribbean Fisheries Institute conference in Grand Cayman, Cayman Islands.

food choices can also be influenced by the nutritional quality of macroalgae (Montgomery and Gerking 1980, Dromard et al. 2015). The nutritional quality can be evaluated by the concentrations of macronutrients (Montgomery and Gerking 1980). High concentrations of proteins, lipids and soluble carbohydrates generally indicate a high nutritional quality because these compounds are readily metabolically available for consumers and provide a large proportion of energy. On the contrary, insoluble carbohydrates are more difficult to digest. Indeed, their high concentration indicates a low nutritional quality. While several studies have investigated the chemical composition of macroalgae (Dawes 1986, Robledo and Freile Pelegrín 1997), these results have rarely been correlated to the food preferences of herbivorous fishes (Montgomery and Gerking 1980, Wilson 2002, Dromard et al. 2015).

In the present study, different genera and species of

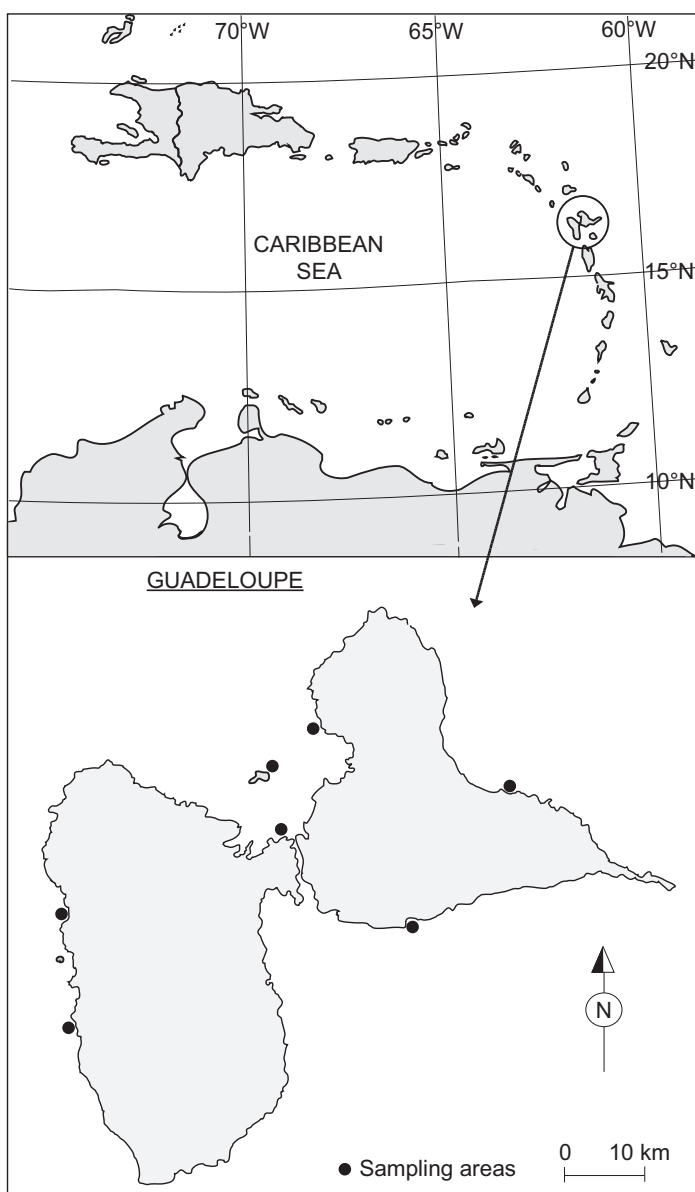


FIGURE 1. Location of the sampling areas in Guadeloupe, Lesser Antilles.

non-calcified macroalgae of Guadeloupean coral reefs were analyzed and grouped according to their biochemical composition and therefore by their nutritional interests for herbivores. The results were then compared with the known food preferences of Caribbean herbivorous fishes. While the nutritional quality of macroalgae can also be measured with the nitrogen content (Barile et al. 2004), this analysis was beyond the scope of the present study.

MATERIALS AND METHODS

Sampling

Samples of macroalgae were collected in 2010 along the coasts of Guadeloupe, Lesser Antilles (16°15'N; 61°30'W) (Figure 1). Fifteen species and one genus of non-calcified macroalgae were collected by SCUBA diving on reefs and seagrass beds between 10 and 15 m depth. Two to 6 replicates were collected for each genus or species (Table 1).

Biochemical analyses

Concentrations of proteins were measured according to a modified version of the method of Lowry et al. (1951). Soluble and insoluble carbohydrates were determined by a modified version of the technique of Dubois et al. (1956). Finally, lipids were extracted and measured following the method of Bligh and Dyer (1959). Ash content was obtained by combusting samples at 500°C for 5 h in a muffle furnace and reweighing after cooling. All concentrations (mg/g) and percentages (%) were expressed on a dry weight basis.

Statistical analysis

A hierarchical clustering analysis on principal components (HCPC) was done to group the different species and genus of macroalgae according to their biochemical characteristics (concentrations of ash, proteins, lipids, and soluble and insoluble carbohydrates). This function combines principal components analysis, hierarchical clustering and partitioning to better visualize and highlight the similarities of biochemical composition between macroalgae. Statistical analyses were done with R version 2.14.1 (library FactoMineR, <http://factominer.free.fr/index.html>). All replicates were taken into account in this analysis and similar species were then encircled by hand in the graph to identify and situate the different replicates of each species.

RESULTS AND DISCUSSION

Three groups of macroalgae were identified according to their biochemical contents and their nutritional composition (Figure 2). The first group was composed of *Ceramium cf nitens*, *Ulva cf lactuca* and *Lobophora cf variegata* (Figure 2, green text), which presented a high nutritional quality due to their high concentrations of proteins and soluble carbohydrates, with a low proportion of ash. According to previous studies, herbivorous fishes prefer these macroalgae. Paul and Hay (1986) conducted several feeding preference assays in different reefs of the Florida Keys; in 2 sites, *Ceramium*

TABLE 1. Mean concentration of ash, proteins, lipids, soluble and insoluble carbohydrates (mg/g \pm standard error, with the % of dry matter below in parenthesis) measured in macroalgae collected from coral reefs in Guadeloupe. *n* is the number of samples (Carb: carbohydrates)

Species - Genus - Phyla	Common Name	n	Ash	Proteins	Lipids	Insoluble carb.	Soluble carb.
CHLOROPHYTA		18	475.6 \pm 129.6	50.8 \pm 53.4	36.8 \pm 24.1	105.7 \pm 33.2	42.7 \pm 34.1
			(66.0 \pm 13.4)	(7.4 \pm 8.2)	(5.3 \pm 3.7)	(15.0 \pm 5.3)	(6.2 \pm 5.3)
<i>Caulerpa cupressoides</i>	Cactus tree alga	6	433.7 (62.2)	26.9 \pm 5.2 (3.9)	54.1 \pm 7.3 (7.9)	145.2 \pm 14.0 (21.1)	33.6 \pm 5.5 (4.9)
<i>Caulerpa racemosa</i>	Sea grapes	3	651.6 (83.7)	15.0 \pm 1.7 (1.9)	21.9 \pm 1.5 (2.8)	75.0 \pm 15.7 (9.6)	15.7 \pm 5.2 (2.0)
<i>Caulerpa sertularioides</i>	Green feather alga	3	443.3 (67.5)	21.0 \pm 1.5 (3.2)	67.0 \pm 17.5 (10.1)	97.1 \pm 6.4 (14.8)	29.3 \pm 5.5 (4.4)
<i>Dictyosphaeria cavernosa</i>	Green bubble weed	3	602.0 (76.4)	51.2 \pm 6.2 (6.5)	14.3 \pm 2.5 (1.8)	90.5 \pm 11.3 (11.5)	29.5 \pm 8.5 (3.8)
<i>Ulva cf lactuca</i>	Sea lettuce	3	289.2 (44.1)	163.6 \pm 5.9 (24.9)	9.4 \pm 0.9 (1.4)	81.1 \pm 31.6 (12.2)	114.6 \pm 6.8 (17.4)
RHODOPHYTA		15	510.8 \pm 159.6	27.5 \pm 19.3	15.1 \pm 8.9	56.5 \pm 12.2	122.6 \pm 65.3
			(68.2 \pm 17.1)	(4.0 \pm 3.5)	(2.1 \pm 1.1)	(7.8 \pm 2.1)	(17.9 \pm 12.2)
<i>Acanthophora spicifera</i>	Spiny seaweed	3	617.7 (79.5)	22.9 \pm 1.8 (2.9)	11.1 \pm 0.4 (1.4)	38.3 \pm 2.2 (4.9)	87.7 \pm 19.6 (11.2)
<i>Ceramium cf nitens</i>	-	3	212.1 (35.6)	63.4 \pm 7.8 (10.6)	16.3 \pm 1.0 (2.7)	62.5 \pm 9.6 (10.4)	242.6 \pm 6.3 (40.6)
<i>Chondria sp.</i>	-	3	567.0 (76.4)	15.4 \pm 1.2 (2.1)	11.6 \pm 1.2 (1.6)	60.7 \pm 16.1 (8.2)	88.1 \pm 10.8 (11.9)
<i>Hypnea cf musciformis</i>	Hypnea	3	524.6 (72.0)	12.9 \pm 0.3 (1.8)	6.0 \pm 0.1 (0.8)	61.5 \pm 6.9 (8.4)	123.8 \pm 7.3 (17.0)
<i>Laurencia cf chondrioides</i>	Laurencia	3	632.8 (77.5)	23.1 \pm 1.0 (2.8)	30.6 \pm 5.3 (3.7)	59.6 \pm 3.6 (7.3)	71.0 \pm 10.4 (8.7)
PHAEOPHYTA			359.1 \pm 54.0	65.0 \pm 34.9	59.1 \pm 54.5	77.0 \pm 22.1	27.7 \pm 12.8
			(61.5 \pm 8.3)	(10.9 \pm 5.6)	(9.7 \pm 8.3)	(13.2 \pm 3.7)	(4.7 \pm 2.0)
<i>Dictyota cf pulchella</i>	Dictyota	6	339.2 (53.0)	41.6 \pm 11.8 (6.5)	139.9 \pm 8.7 (21.8)	84.1 \pm 4.0 (13.1)	35.5 \pm 14.3 (5.5)
<i>Lobophora cf variegata</i>	Encrusting fan-leaf alga	3	351.1 (54.4)	121.0 \pm 5.8 (18.7)	20.5 \pm 1.4 (3.2)	112.9 \pm 14.3 (17.4)	40.0 \pm 0.7 (6.2)
<i>Padina cf sanctae-crucis</i>	Peacock algae	3	423.1 (72.5)	47.8 \pm 7.1 (8.2)	21.2 \pm 1.5 (3.6)	73.6 \pm 0.9 (12.6)	18.2 \pm 9.1 (3.1)
<i>Sargassum cf hystrix</i>	Sargassum	3	324.8 (62.2)	86.2 \pm 7.0 (16.5)	28.2 \pm 1.2 (5.4)	58.6 \pm 13.9 (11.2)	24.2 \pm 9.9 (4.6)
<i>Sargassum cf polyceratium</i>	Sargassum	2	265.7 (65.2)	11.8 \pm 1.8 (2.9)	29.7 \pm 1.1 (7.3)	75.2 \pm 29.8 (18.2)	26.3 \pm 1.6 (6.4)
<i>Turbinaria turbinata</i>	Saucer leaf alga	3	439.5 (71.5)	87.5 \pm 7.4 (14.2)	24.6 \pm 2.7 (4.0)	49.6 \pm 4.8 (8.1)	13.7 \pm 0.3 (2.2)

subtile and *C. nitens* appeared as the most consumed species with 100% and 75% of algae, respectively, eaten during the experiment. In a similar experiment, *Ulva lactuca* presented 100% loss to fish grazing (Littler et al. 1983). Finally, *Lobophora variegata* was consumed in the experiments of Lewis (1985), with a loss of 100% of the initial weight. A positive correlation between the nutritional quality of that group of macroalgae and the food preferences of herbivores on coral reef was thus observed.

The second group in our study, constituted by *Dictyota cf pulchella*, *Caulerpa cupressoides*, *Caulerpa sertularioides* and *Sargassum cf polyceratium* (Figure 2, red text), presented inter-

mediate nutritional qualities due to higher concentrations of lipids (high energetic compounds) but also of insoluble carbohydrates (low energetic compounds). Dictyotaceae and Caulerpaceae are often described as low preference species due to their amount of secondary metabolites (Lewis 1985, Paul and Hay 1986). *Caulerpa cupressoides* and *C. sertularioides* were found to contain both caulerpicin and caulerpin, while *Dictyota* spp. produces complex mixtures of terpenoids, acetogenins and terpenoids—aromatic compounds (Norris and Fenical 1982, Hay and Fenical 1988). These molecules have been identified as deterrents against herbivory (Hay 1991). The susceptibility of grazing on *Sargassum*

spp. is more variable. Some studies showed that *Sargassum* spp. could be highly consumed by herbivorous fishes (*S. polyceratium* in Lewis 1985, *S. vulgare* in Ogden 1976, *Sargassum* spp. in Mantyka and Bellwood 2007). However, in Littler et al. (1983), *S. polyceratium* was among the least vulnerable to herbivory when fixed on a weighted grid (<10% lost to grazing), but presented a low resistance to herbivory when placed midway in the water column (96.5% consumed). Thus, the nutritional quality of these 4 species in the genus *Sargassum* appeared to be weakly correlated to their susceptibility to be eaten. Undoubtedly, other factors may be involved such as the presence of deterrent molecules or the composition of the herbivorous fish population (Scaridae [parrotfishes] near the bottom vs Kyphosidae [sea chubs] in the water column, Littler et al. 1983).

The other species and genus of macroalgae collected in this study were grouped in a third category (Figure 3, black text), which was characterized by a high proportion of ash, thus presenting a low nutritional quality. In this group, some species are known to be avoided by herbivorous fishes such as *Dictyosphaeria cavernosa* (Paul and Hay 1986), results which correlated to the biochemical composition of these macroalgae. However, the majority of the other species of this group are cited as preferred macroalgae for some herbivorous fishes such as *Acanthophora spicifera*, *Padina* spp., *Chondria* spp., *Hypnea* spp. and *Laurencia* spp. (Littler et al. 1983, Lewis 1985, Paul and Hay 1986, Mantyka and Bellwood 2007). For these species, the biochemical composition was not related to the food preference of fishes.

For one species, *Sargassum cf hytrix*, the 3 replicates were spread into 2 groups (indicated in red and green in Figure 2). Indeed, it was not possible to cluster this species with a specific group.

The present study indicates that the biochemical composition in macronutrients only partially explains the food choice made by herbivorous fishes. The consumption of macroalgae probably depends on a large suite of factors, including the nutritional quality. Firstly, the presence of deterrent molecules is an important factor to explain alimentary choices

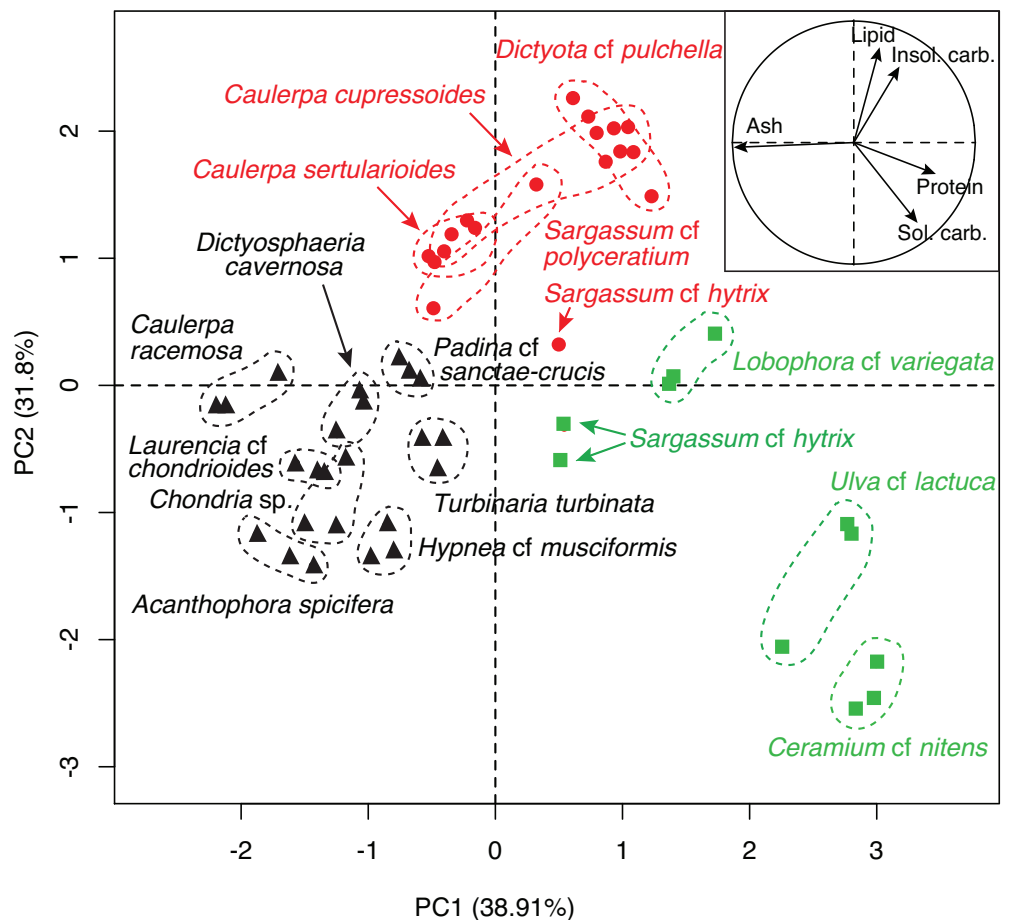


FIGURE 2. Results of the hierarchical clustering analysis plotted on principal components of each replicate sample. Different symbols and colors (red circles, green squares, black triangles) indicate the 3 groups of macroalgae identified with the cluster analysis. Envelopes were then drawn by hand on the figure to encircle the different replicates of each species. Prot: proteins, Insol. carb: insoluble carbohydrates, Sol. carb: soluble carbohydrates

of fishes. According to Paul and Hay (1986), 25 species of low preference macroalgae (<25% eaten) produced secondary metabolites, while only 9 did not. In contrast, only 4 species of high preference algae (>75% eaten) produced secondary metabolites, while 16 species did not. The link between the presence of secondary metabolites and the intensity of grazing has been demonstrated before (Norris and Fenical 1982, Lewis 1985, Hay 1991). Secondly, the structure of macroalgae is also a factor influencing the probability of grazing. Sheet-like and filamentous forms are more likely to be eaten than jointed erected calcareous or crustose forms, which are generally avoided because they are more difficult to graze on (Steneck and Watling 1982, Littler et al. 1983). In the present study, we focused our results on non-calcified species. Different forms of non-calcified macroalgae have been described (filamentous algae, foliose or sheet-like algae, corticated or coarsely-branched macrophytes and leathery macrophytes), leading to different susceptibility to be consumed by fishes (Steneck and Watling 1982, Littler et al. 1983). Thirdly, in the present study, only the concentrations of macronutrients have been measured, although oth-

er compounds such as vitamins or essential trace elements could be important in the feeding choice of herbivores. In the same way, the concentrations of carbon (C%), nitrogen (N%) or phosphorus (P%) were not measured in the present study, but these elements can be used as proxy of the nutritional quality of macroalgae, in calculating the C:N:P ratios (Lapointe et al. 2005). Fourthly, the palatability of macroalgae can vary among individuals (intra-specific variability), reproductive conditions, age of tissue or seasons (Montgomery and Gerking 1980).

To conclude, the present study indicates that the biochemical composition in macronutrients only partially explains the food choice made by herbivorous fishes. The consumption of macroalgae by herbivores also depends on the presence of deterrent molecules, the composition in micronutrients, their morphology, and their palatability. It is likely that algae preference is a combination of all these factors. Further investigations are needed to understand all the factors that influence the grazing of macroalgae species by herbivorous fishes on coral reefs.

ACKNOWLEDGEMENTS

We gratefully thank S. Cordonnier and L. Urvoix, from Université des Antilles, for their help in field sampling and M.F. Fontaine, from CNRS, for her help in biochemical analyses.

LITERATURE CITED

- Barile, P.J., B.E. Lapointe, and T.R. Capo. 2004. Dietary nitrogen availability in macroalgae affects growth of the sea hare *Aplysia californica* (Opisthobranchia: Anaspidea). *Journal of Experimental Marine Biology and Ecology* 303(1):65–78.
- Bellwood, D.R., T.P. Hughes, C. Folke, and M. Nyström. 2007. Confronting the coral reef crisis. *Nature* 429:827–833.
- Bligh, E.G. and W.J. Dyer. 1959. A rapid method of total lipid extraction and purification. *Canadian Journal of Biochemistry and Physiology* 37:911–917.
- Burkpile, D.E. and M.E. Hay. 2010. Impact on herbivore identity on algal succession and coral growth on a Caribbean reef. *PLoS ONE* 5(1):e8963. <http://doi.org/10.1371/journal.pone.0008963>
- Burkpile, D.E. and M.E. Hay. 2011. Feeding complementarity versus redundancy among herbivorous fishes on a Caribbean reef. *Coral Reefs* 30:351–362. <http://doi.org/10.1007/s00338-011-0726-6>
- Dawes, C.J. 1986. Seasonal proximate constituents and caloric values in seagrass and algae on the West Coast of Florida. *Journal of Coastal Research* 2:25–32.
- Done, T.J. 1992. Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247:121–132. <http://doi.org/10.1007/BF00008211>
- Dromard, C.R., Y. Bouchon–Navaro, M. Harmelin–Vivien, and C. Bouchon. 2015. Diversity of trophic niches among herbivorous fishes on a Caribbean reef (Guadeloupe, Lesser Antilles), evidenced by stable isotope and gut content analyses. *Journal of Sea Research* 95:124–131. <http://doi.org/10.1016/j.seares.2014.07.014>
- Dubois, M., K.A. Gilles, J.K. Hamilton, P.A. Rebers, and F. Smith. 1956. Colorimetric method for determination of sugars and related substances. *Analytical Chemistry* 28:350–356. <http://doi.org/10.1021/ac60111a017>
- Hay, M.E. 1991. Fish–seaweed interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey. In: P.F. Sale, ed. *The Ecology of Fishes on Coral Reefs*, Academic Press, New York, NY, USA, p. 96–119. <http://dx.doi.org/10.1016/B978-0-08-092551-6.50010-6>
- Hay, M.E. and W. Fenical. 1988. Marine plant–herbivore interactions: the ecology of chemical defense. *Annual Review of Ecology and Systematics* 19:111–45.
- Hughes, T.P. 1994. Catastrophes, phase shifts and large–scale degradation of a Caribbean coral reef. *Science* 265:1547–1551.
- Kopp, D., Y. Bouchon–Navaro, S. Cordonnier, A. Haouissée, M. Louis, and C. Bouchon. 2010. Evaluation of algal regulation by herbivorous fishes on Caribbean coral reefs. *Helgolander Marine Research* 64:181–190. <http://doi.org/10.1002/aqc.1118>
- Lapointe, B.E., P.J. Barile, C.S. Yentsch, M.M. Littler, D.S. Littler, and B. Kakuk. 2004. The relative importance of nutrient enrichment and herbivory on macroalgal communities near Norman’s Pond Cay, Exumas Cays, Bahamas: A natural enrichment experiment. *Journal of Experimental Marine Biology and Ecology* 298:275–301
- Lapointe, B.E., P.J. Barile, M.M. Littler, D.S. Littler, B.J. Bedford, and C. Gasque. 2005. Macroalgal blooms on southeast Florida coral reefs: I. Nutrient stoichiometry of the invasive green alga *Codium isthmocladum* in the wider Caribbean indicates nutrient enrichment. *Harmful Algae* 4:1092–1105.
- Ledlie, M.H., N.A.J. Graham, J.C. Bythell, S.K. Wilson, S. Jennings, N.V.C. Polunin, and J. Hardcastle. 2007. Phase shifts and the role of herbivory in the resilience of coral reefs. *Coral Reefs* 26:641–653. <http://doi.org/10.1007/s00338-007-0230-1>
- Lessios, H.A., D.R. Robertson, and J.D. Cubit. 1984. Spread of *Diadema* mass mortality through the Caribbean. *Science* 226:335–37.
- Lewis, S.M. 1985. Herbivory on coral reefs: algal susceptibility to herbivorous fishes. *Oecologia* 65:370–375. <http://doi.org/10.1007/BF00378911>

- Lewis, S.M. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecological Monographs* 56:184–200.
- Littler, M.M., P.R. Taylor, and D.S. Littler. 1983. Algal resistance to herbivory on a Caribbean barrier reef. *Coral Reefs* 2:111–118. <http://doi.org/10.1007/BF02395281>
- Lowry, O.H, N.J. Rosenbrough, A.L. Farr, and R.J. Randall. 1951. Protein measurement with the folin. *Journal of Biological Chemistry* 193:265–275. [http://doi.org/10.1016/0304-3894\(92\)87011-4](http://doi.org/10.1016/0304-3894(92)87011-4)
- Lubchenco, J. and S.D. Gaines. 1981. A unified approach to marine plant–herbivore interactions. I. Populations in communities. *Annual Review of Ecology and Systematics* 12:405–437
- Mantyka, C.S. and D.R. Bellwood. 2007. Direct evaluation of macroalgal removal by herbivorous coral reef fishes. *Coral Reefs* 26:435–442. <http://doi.org/10.1007/s00338-007-0214-1>
- 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.
- McManus, J.W. and J.F. Polsenberg. 2004. Coral–algal phase shifts on coral reefs: ecological and environmental aspects. *Progress in Oceanography* 60:263–279. <http://doi.org/10.1016/j.pocean.2004.02.014>
- Montgomery, W.L. and S.D. Gerking. 1980. Marine macroalgae as foods for fishes: an evaluation of potential food quality. *Environmental Biology of Fishes* 5:143–153. <http://doi.org/10.1007/BF02391621>
- Norris, J.N. and W. Fenical. 1982. Chemical defense in tropical marine algae. *Smithsonian Contributions to the Marine Sciences* 12:417–431.
- Ogden, J.C. and P.S. Lobel. 1978. The role of herbivorous fishes and urchins in coral reef communities. *Environmental Biology of Fishes* 3:49–63. <http://doi.org/10.1007/BF00006308>
- Ogden, J.C. 1976. Some aspects of herbivore–plant relationships on Caribbean reefs and seagrass beds. *Aquatic Botany* 2:103–16. [http://doi.org/10.1016/0304-3770\(76\)90013-9](http://doi.org/10.1016/0304-3770(76)90013-9)
- Paul, V.J. and M.E. Hay. 1986. Seaweed susceptibility to herbivory: chemical and morphological correlates. *Marine Ecology Progress Series* 33:255–64.
- Plass–Johnson, J.G., C.D. McQuaid, and J.M. Hill. 2013. Stable isotope analysis indicates a lack of inter– and intra–specific dietary redundancy among ecologically important coral reef fishes. *Coral Reefs* 32:429–440.
- Randall, J.E. 1967. Food habits of reef fishes in the West Indies. *Studies in tropical Oceanography* 5:665–847.
- Robledo, D. and Y. Freile Pelegrín. 1997. Chemical and mineral composition of six potentially edible seaweed species of Yucatán. *Botanica Marina* 40:301–306. <http://doi.org/10.1515/botm.1997.40.1-6.301>
- Steneck, R.S. and L. Watling. 1982. Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. *Marine Biology* 68:299–319. <http://doi.org/10.1007/BF00409596>
- Targett, N.M., T.E. Targett, N.H. Vrolijk, and J.C. Ogden. 1986. Effect of macrophyte secondary metabolites on feeding preferences of the herbivorous parrotfish *Sparisoma radians*. *Marine Biology* 92:141–148. <http://doi.org/10.1007/BF00392756>
- Wilson, S. 2002. Nutritional value of detritus and algae in blenny territories on the Great Barrier Reef. *Journal of Experimental Marine Biology and Ecology* 271:155–169. [http://doi.org/10.1016/S0022-0981\(02\)00035-7](http://doi.org/10.1016/S0022-0981(02)00035-7)