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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 antilarum*. 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 macrolgae 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 genus, 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 synthetize repellent molecules, which deter herbivores and inhibit grazing in influencing their palatability (Paul and Hay 1986, Targett et al. 1986, Hay and Fenical 1988). Finally, food choices can also be orientated 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 made by herbivorous fishes (Montgomery and Gerking 1980, Wilson 2002, Dromard et al. 2015). The nutritional quality of macroalgae can also be measured with the nitrogen content (Barile et al. 2004) but this factor has not been measured in the present study.

In the present study, different genera and species of 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.

MATERIAL ET METHODS

Sampling

Samples of macroalgae were collected in 2010 along the coasts of Guadeloupe, Lesser Antilles (16°15′N; 61°30′W) (Figure 1). 15 species and 1 genera of non-calcified macroalgae were collected by SCUBA diving on reefs and seagrass beds between 10 and 15 m depth. Two to six 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 five hours in a muffle furnace and reweighing after cooling. All concentrations ($mg.g^{-1}$) 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 (library FactorMineR). All replicates were taken into account in this analysis and similar species were then enveloped 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 by *Ceramium* cf *nitens*, *Ulva* cf *lactuca* and *Lobophora* cf *variegata* 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 preferences assays in different reefs of Florida Keys. In two sites, *Ceramium subtile* and *C. nitens* appeared as the most consumed species with 100% and 75% of algae eaten after the experiment. In a similar experiment, *Ulva lactuca* presented 100% loss to fish grazing (Littler et al. 1983). Finally, *Lobophora variegata* was highly 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 constituted by *Dictyota* cf *pulchella*, *Caulerpa cupressoides*, *C. sertularioides* and *Sargassum* cf *polyceratium*, presented intermediate 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 for *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). 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 four species or genus appeared to be weakly correlated to their susceptibility to be eaten. Undoubtedly, other factors seemed to 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 were grouped in a third category, which was characterized by a high proportion of ash and presented consequently 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). In this situation, the food preference is 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 three replicates were spread into two groups (the first and the second one, 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 thus 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 panel of factors, including the nutritional quality. Firstly, the presence of deterrent molecules is an important factor to explain alimentary choices of fishes. According to Paul and Hay (1986), 25 species of low preference (<25% eaten) produced secondary metabolites, while only 9 did not. In contrast, only four 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 more difficult to graze (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 in macronutrients have been measured. However, other 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 with individual (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.

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TABLES

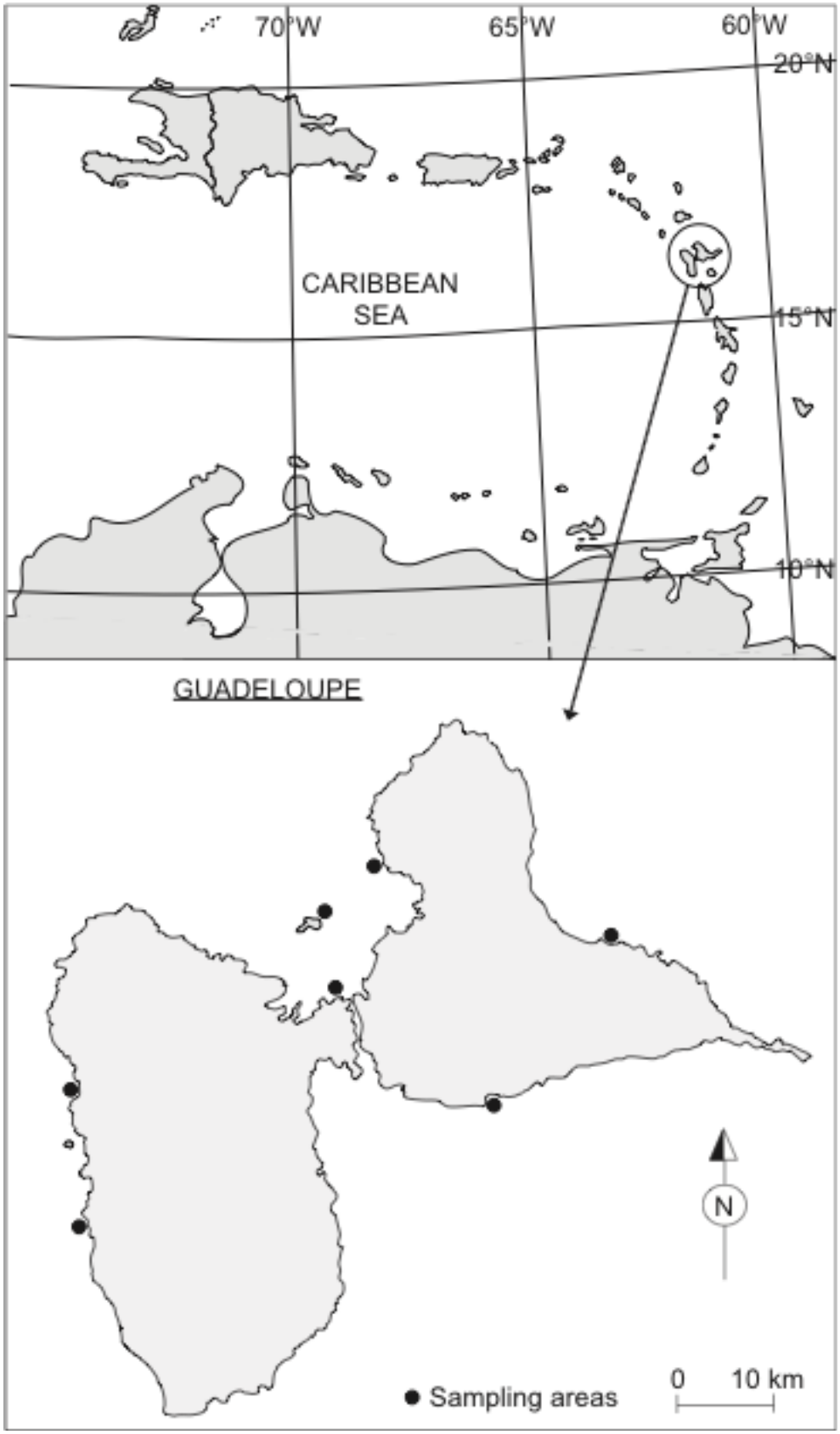
Table 1 Mean concentration of ash, proteins, lipids, soluble and insoluble carbohydrates ($mg.g^{-1}$ ± standard error and % of dry matter into parenthese), measured in macroalgae. n is the number of samples (Carb: carbohydrates).

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

FIGURE LEGEND

Figure 1 Location of the sampling areas in Guadeloupe.
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 three groups of macroalgae identified with the cluster analysis. Envelopes were then drawn by hand on the figure to situate the different replicates of each species. Prot: proteins, Insol. carb: insoluble carbohydrates, Sol. carb: soluble carbohydrates

FIGURE


70°W
65°W
60°W
20°N
15°N
10°N
CARIBBEAN
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GUADELOUPE
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Sampling areas
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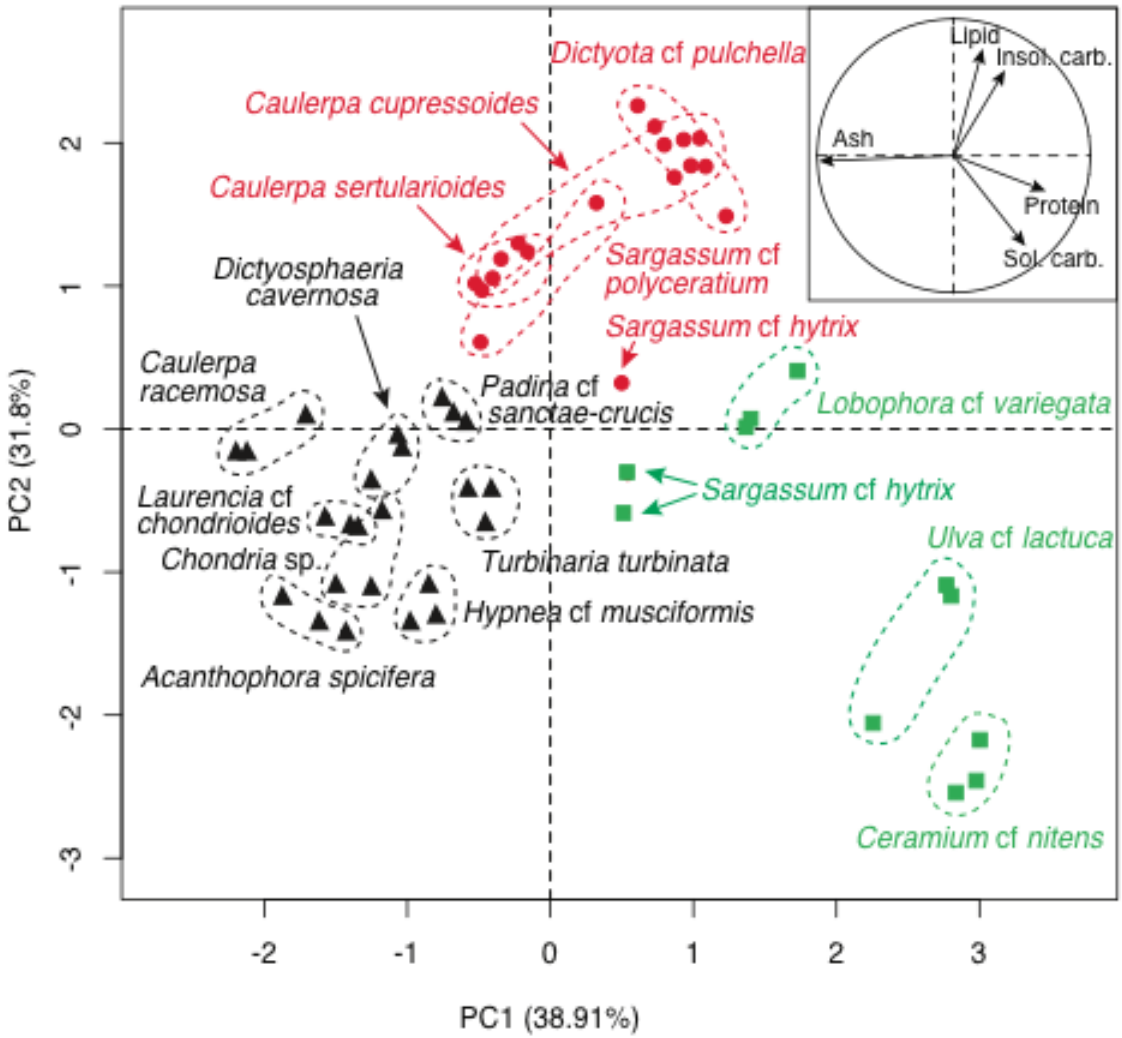
10 km


Dictyota cf pulchella
Caulerpa cupressoides
Caulerpa sertularioides
Dictyosphaeria cavernosa
Sargassum cf polyceratium
Sargassum cf hytrix
Caulerpa racemosa
Padina cf sanctae-crucis
Lobophora cf variegata
Sargassum cf hytrix
Laurencia cf chondrioides
Chondria sp.
Turbinaria turbinata
Ulva cf lactuca
Hypnea cf musciformis
Acanthophora spicifera
Ceramium cf nitens
Lipid
Insol. carb.
Ash
Protein
Sol. carb.
PC2 (31.8%)
PC1 (38.91%)
-3
-2
-1
0
1
2
-2
-1
0
1
2
3