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MACROECOLOGIA E ASPECTOS QUÍMICOS DE MACROALGAS DO ATLÂNTICO SUL ORIENTAL

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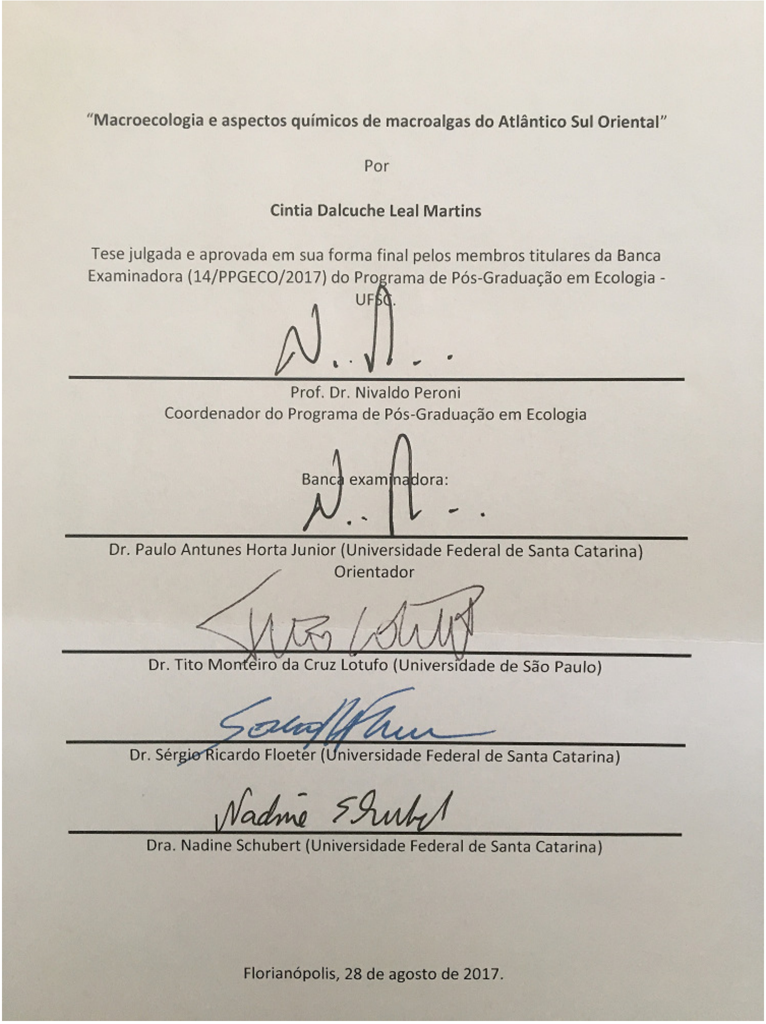

“Macroecologia e aspectos químicos de macroalgas do Atlântico Sul Oriental”

Por

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RESUMO

A distribuição e a abundância dos produtores primários marinhos é resultado de uma combinação de controles do tipo bottom-up, principalmente representados pela temperatura da superfície do mar (SST), radiação fotossinteticamente ativa (PAR) e disponibilidade de nutrientes, e controles do tipo top-down, representados pelas interações biológicas, como por exemplo herbivoria e competição. Além de exercer influência sobre a estruturação de comunidades, estes fatores ambientais e biológicos podem ainda ser determinantes sobre o comportamento bioquímico de uma comunidade, modulando direta ou indiretamente a síntese de metabólitos primários e secundários. Considerando que a biosíntese destes metabólitos pode ser uma função direta do estado ecofisiológico de um organismo, o perfil químico de uma comunidade pode representar uma fonte alternativa de informação de padrões ecológicos em diferentes escalas e ecossistemas. Esta tese apresenta diferentes abordagens em relação à influência de fatores ambientais e biológicos sobre a estruturação de comunidades de macroalgas marinhas e sobre a composição química das mesmas, tanto em escala local quanto em escala regional. Sendo assim, esta tese está dividida em três capítulos: (1) "*Seaweed chemical diversity: an additional and efficient tool for coastal evaluation*", que investigou a relação entre a diversidade ecológica e a diversidade química de comunidades de macroalgas marinhas, usando medidas de impacto antrópico em escala local como fatores preditores; (2) "*Macroecological drivers of algal turf assemblages of the Southwestern Atlantic*", que descreveu a composição de espécies e respectivas abundâncias das comunidades de algas formadoras de turf e investigou o papel dos potenciais fatores macroecológicos preditores dos padrões de diversidade, ao longo de um gradiente latitudinal de mais de 4000 km; e (3) "*Spatial variability of chemical compounds in turf assemblages from Southwestern Atlantic*", que quantificou as concentrações de compostos químicos em assembléias de turf, comparou seus valores entre diferentes regiões ao longo de um gradiente latitudinal e explorou a influência dos fatores macroecológicos sobre os padrões químicos apresentados. Os resultados indicaram que: (1) a riqueza e a abundância de metabólitos primários e secundários produzidos por comunidades de macroalgas marinhas é maior em ambientes cuja diversidade de espécies também é maior; (2) as assembleias de turf são dominadas por algas calcárias articuladas, especialmente *Jania* sp. e *Amphiroa* sp, e os fatores ambientais determinantes para a sua estruturação ao longo do gradiente latitudinal analisado foram SST e PAR; e (3) as maiores concentrações de carboidratos de reserva e de compostos fenólicos em algas formadoras de turf encontram-se nas regiões temperada quente e extremo tropical, respectivamente. A síntese de açúcares, carboidratos de reserva e compostos fenólicos foi determidada pelos fatores SST e PAR e está relacionada à biomassa e à riqueza do turf. Os resultados deste trabalho confirmam que os fatores preditores dos padrões de diversidade das comunidades de macroalgas, sejam elas formadoras de dossel ou formadoras de turf, são também preditores da expressão metabólica de seus organismos constituintes.

Palavras-chave: Macroalga. Turf. Estrutura de comunidade. Composição química. Gradiente latitudinal.

ABSTRACT

The distribution and abundance of marine primary producers is a result of the combination of bottom-up controls, mainly represented by sea surface temperature (SST), photosynthetically active radiation (PAR) and nutrient availability, and top-down controls, represented by biological interactions, such as herbivory and competition. Besides influencing the structuring of communities, these environmental and biological factors can also be determinant on the biochemical performance of a community, modulating directly or indirectly the synthesis of primary and secondary metabolites. Considering that the biosynthesis of these metabolites may represent a direct function of the ecophysiological state of an organism, the chemical profile of a community may represents an alternative source of information on ecological patterns at different scales and ecosystems. This thesis presents different approaches regarding the influence of environmental and biological factors on the structuring of marine macroalgae communities and their chemical composition, both locally and regionally. Thus, this thesis is divided into three chapters: (1) "Seaweed chemical diversity: an additional and efficient tool for coastal evaluation", which investigated the relationship between ecological diversity and chemical diversity of marine macroalgae communities, using as drivers measures of anthropogenic impact on local scale; (2) "Macroecological drivers of algal turf assemblages of the Southwestern Atlantic", which described the species composition and respective abundances of turf-forming algae communities and investigated the role of potential macroecological factors driving diversity patterns over a latitudinal gradient of more than 4000 km; and (3) "Spatial variability of chemical compounds in turf assemblages from Southwestern Atlantic", which quantified chemical compounds concentrations in turf assemblages, compared their values across different regions along a latitudinal gradient and explored the influence of macroecological drivers on chemical patterns. The results indicated that: (1) richness and abundance of primary and secondary metabolites produced by marine macroalgae communities is greater in environments with higher species diversity; (2) turf assemblages are dominated by articulated calcareous algae, especially *Jania* sp. and *Amphiroa* sp., and the environmental drivers related to their structuring along the latitudinal gradient were SST and PAR; and (3) the highest concentrations of reserve carbohydrates and phenolic compounds in turf-forming algae are found in the warm temperate and extreme tropical regions, respectively. The synthesis of sugars, reserve carbohydrates and phenolic compounds was determined by the factors SST and PAR and was related to biomass and turf richness. The results of this work confirm that the drivers determining diversity patterns of macroalgal communities, be they canopy forming or turf forming, are also drivers of the metabolic expression of their constituent organisms

Keywords: Macroalgae. Turf. Community structure. Chemical composition. Latitudinal gradient.

"O topo da inteligência é alcançar a humildade".
Texto Judaico

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INTRODUÇÃO GERAL

A elucidação de processos dentro de diferentes escalas espaciais tem se tornado uma questão nevrálgica dentro da ecologia, uma vez que os fatores responsáveis por estabelecer padrões biogeográficos, bem como a identificação de seus mecanismos causais não estão totalmente compreendidos (Levin 1992, Peterson & Parker 1998, Gardner et al. 2001). Um dos mais importantes fatores macroecológicos utilizado na predição de padrões biogeográficos é a temperatura. Para os produtores primários marinhos, a temperatura da água do mar (ST) está diretamente relacionada aos limites geográficos de ocorrência de espécies. Muitos deles podem tolerar variações de temperatura no ambiente, porém o resfriamento ou o aquecimento da água influenciará seu ciclo de vida, sua reprodução e os processos relacionados com a colonização de substrato e o seu desenvolvimento (Van Den Hoek 1982, Lüning 1990, De Faveri et al. 2015). Além da ST, a radiação fotossinteticamente ativa (PAR), que constitui parte da radiação solar, tem sua disponibilidade no ambiente relacionada com a latitude, assim como com fatores locais como transparência da água e profundidade a que um organismo se encontra. Como é recurso primário para o processo de fotossíntese, também compreende um fator chave e muitas vezes limitante para a produção primária (Graham et al. 2009, Hanelt & Figueroa 2012) e um fator adicional na determinação de padrões latitudinais (Eggert 2012). Além dos fatores supracitados, os nutrientes inorgânicos dissolvidos na água do mar (DINs) também são responsáveis por influenciar a fisiologia dos produtores primários marinhos e determinar sua distribuição em escala global. A maior ou menor disponibilidade de fontes de nitrogênio e fosfato podem regular a sobrevivência, o crescimento e a reprodução destes organismos (Steneck et al. 2002, Gordillo 2012). Grandes concentrações de nutrientes podem estar presentes naturalmente no ambiente marinho em áreas de ressurgência ou próximas a foz de grandes rios, ou podem ainda ser influenciadas por estressores locais (Scherner at al. 2012, 2013, De Faveri et al. 2015), quase sempre relacionados a atividades antrópicas em áreas costeiras. Descargas de efluentes domésticos e industriais em grandes conglomerados urbanos são capazes de produzir grandes plumas em regiões costeiras, aumentando drasticamente a concentração local de DINs e reduzindo, por exemplo, os valores de PAR incidente sobre o bentos marinho. Estes três fatores citados acima representam os principais preditores abióticos na estruturação de comunidades de produtores primários em ambientes marinhos, determinando os limites de ocorrência e abundância de espécies em diferentes escalas de observação. Todavia, diferenças na estrutura de comunidades podem também ser resultado de interações biológicas das mais diversas. A herbivoria e a competição são dois dos mais importantes processos biológicos responsáveis pela sucessão e heterogeneidade dentro de uma comunidade (Steneck & Dethier 1994). Em resumo, é possível afirmar que a distribuição e a abundância de organismos produtores primários é resultado de uma combinação de controles do tipo bottom-up, principalmente representados pela temperatura, irradiância e disponibilidade de nutrientes, e controles do tipo top-down, especialmente representado pela herbivoria (Littler et al. 2006). Em baixas latitudes, as interações biológicas são hipoteticamente mais intensas e, portanto, mais importantes na condução de processos evolutivos e seus padrões macroecológicos resultantes. Em contrapartida, os fatores ambientais físico/químicos ou abióticos parecem influenciar mais fortemente a estruturação de comunidades de produtores primários em maiores latitudes (Pianka 1966, Wiens & Donoghue 2004, Keith et al. 2014).

Além de influenciar a estruturação de comunidades, estes fatores ambientais e biológicos podem também ser determinantes do comportamento bioquímico da diversidade biológica. Estes fatores modulam, direta ou indiretamente, a síntese de metabólitos primários e secundários de produtores primários marinhos (Yates & Peckol 1993, Cronin & Hay 1996, Peckol et al. 1996, Pavia et al. 1997). Considerando a hipótese de que a produção destes metabólitos é resultado do estado ecofisiológico de um organismo, a variação espacial da ocorrência e abundância destes metabólitos pode representar um descritor importante para compreender mecanismos responsáveis por determinar padrões ecológicos em diferentes escalas, sendo sensíveis a estressores locais e globais. Com base em conceitos e teorias relacionados à diversidade ecológica, a diversidade química pode ser definida pela riqueza e abundância de compostos ou classes químicas produzidos por um organismo, população ou comunidade (Whittaker 1972, Hill 1973, Magurran 1988). Considerando que a biosíntese de tais substâncias é uma função direta do estado ecofisiológico de um organismo, o perfil químico de uma comunidade pode ser considerado uma resposta direta aos diferentes fatores bióticos e abióticos que influenciam sua diversidade e, portanto, representam uma fonte alternativa de informação de padrões ecológicos em diferentes escalas e ecossistemas.

Para que o universo metabolômico possa ser plenamente compreendido é importante que se conheça a estrutura das comunidades em questão. Falando em macroalgas muito se investiu no conhecimento da estrutura formadora de dossel propriamente, enquanto que as algas aparentemente mais efêmeras foram até então negligenciadas. Estas algas formadoras de tapetes de aspectos diversificados que recobrem o substrato são conhecidas como turf e se destacam por sua fundamental importância ecológica, especialmente em ambientes recifais. Enquanto as algas formadoras de dosséis são organizadas em escalas de centímetros e metros, as populações macroalgais que compõem o turf são estruturadas na escala de milímetros a centímetros. As algas formadoras de turf são frequentemente agrupadas dentro de um único grupo funcional, apesar de sua complexa heterogeneidade, sendo raramente classificadas a nível específico. Poucos trabalhos foram publicados com dados consistentes acerca da composição de espécies e abundância das assembéias de turf e não há registro de estudos desta natureza em escala latitudinal.

Esta tese apresenta diferentes abordagens em relação à influência de fatores ambientais sobre a estruturação de comunidades de macroalgas marinhas e sobre a composição química das mesmas, tanto em escala local quanto em escala regional. Sendo assim, esta tese está dividida em três capítulos. O primeiro capítulo, intitulado "Seaweed chemical diversity: an additional and efficient tool for coastal evaluation" investigou a relação entre a diversidade ecológica e a diversidade química de comunidades de macroalgas marinhas, usando medidas de impacto antrópico em escala local como fatores preditores. Neste capítulo testamos a hipótese de que a diversidade química apresenta comportamento semelhante, sendo influenciada da mesma forma que a diversidade biológica é influenciada por estressores diversos. Respondida esta questão buscamos avaliar se estes padrões se mantinham nas grandes escalas. Portanto, os resultados deste capítulo nos levaram a desenvolver os dois subsequentes, a partir da confirmação de que a produção de metabólitos primários e secundários estava condicionada ao estado ecofisiológico da comunidade e à sua exposição a fatores ambientais estressores. No segundo capítulo, intitulado "Macroecological drivers of algal turf assemblages of the Southwestern Atlantic", descrevemos a composição de espécies e respectivas abundâncias das comunidades de algas formadoras de turf e investigamos o papel dos potenciais fatores macroecológicos preditores dos padrões de diversidade, ao longo de um gradiente latitudinal de mais de 4000 km. Uma das principais pretensões deste segundo capítulo foi estudar as assembléias de turf com maior detalhamento do que como um grupo funcional homogêneo, como usualmente são tratadas. Uma das regras fundamentais da ecologia é entender primeiro o padrão para que possamos investigar o processo (Levin 1992). Considerando essa premissa, desenvolvemos o terceiro capítulo, intitulado "Spatial variability of chemical compounds in turf assemblages from Southwestern Atlantic". Este capítulo teve como principal objetivo verificar se o padrão de resposta sob uma perspectiva metabólica das comunidades de macroalgas em escala local (capítulo 1) também poderia ser observado em escala geográfica regional. Para tanto, quantificamos as concentrações de alguns compostos químicos em assembléias de turf, comparamos seus valores entre diferentes regiões ao longo de um gradiente latitudinal e exploramos a influência dos fatores macroecológicos sobre os padrões químicos apresentados.

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CAPÍTULO 1

Seaweed chemical diversity: an additional and efficient tool for coastal evaluation

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SEAWEED CHEMICAL DIVERSITY: AN ADDITIONAL AND EFFICIENT TOOL FOR COASTAL EVALUATION

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ABSTRACT

Assessment of human impacts on marine ecosystems are usually described by assessing changes in species diversity and abundance. Here we increment this approach with an assessment of primary and secondary metabolites from macroalgal communities at urban and preserved sites in south Brazil. In this way, we propose that the chemical richness and abundance are useful additional source of information about the ecological status of coastal environments. In this paper we investigate whether the chemical diversity of marine macroalgae are affected by environmental changes, such as those caused by coastal urbanization, through the use of thin layer chromatography. Additionally, we compare chemical and biological diversity of macroalgal communities within urban and undeveloped sites along the southern Brazilian coast. Coastlines within protected areas had greater species richness and higher amounts of substances such as chlorophylls, carotenoids and lipids as well as a greater chemical diversity than coasts subjected to multiples stressors from urbanization. We propose that the composition and abundance of primary and secondary metabolites provides useful additional information about the ecological status of coastal environments and improves our understanding of the effects of coastal biodiversity loss due to coastal urbanization.

Key Words: phytobenthic community; natural resources; human impact**;** ecological index, environmental description

1. INTRODUCTION

Variation in the composition and abundance of biological communities and ecosystems are commonly described by assessing changes in the number and abundance of species in different habitats (Lubchenco et al. 1991). However, this approach has limitations; for example values given to species diversity are influenced by taxonomic knowledge and the availability of expertise in applying that knowledge (Magurran 2004). Advances in molecular biology have shown that for many groups the number of cryptic species is enormous (Bickford et al. 2007), making it impossible to accurately assess biological diversity using the traditional approach of biologists identifying organisms using taxonomic keys. Here we examine the use of diversity indexes (Hill et al. 2003; Margalef 1982), for describing the chemical composition of populations and communities as this aspect is understudied (McIntire et al. 1969). Using widely accepted concepts of diversity indexes (Hill 1973; Magurran 1988; Whittaker 1972), chemical diversity can be defined as the richness and abundance of compounds or chemical classes in an organism, population or community. Thus, if biodiversity can be characterized by the diversity of chemical compounds found in a given species, then perhaps a diverse biome is where chemical heterogeneity flourishes. If some populations produce chemically unique substances (Heethoff et al. 2011), often used in chemotaxonomy for species determination (De Paula et al. 2001; Kelecom and Teixeira 1986; Kelecom et al. 1991), the biosynthesis of such substances can be a direct function of metabolism conservation. In this paper we argue that the chemical profile of an organism, population or community also represents an alternative source of information to describe environmental changes or impacts.

Some environmental factors, such as salinity (Ragan and Glombitza 1986; Scherner et al. 2013b), nutrients (Cronin and Hay 1996; Peckol et al. 1996; Yates and Peckol 1993), light (Cronin and Hay 1996), ultraviolet radiation (Pavia et al. 1997) and desiccation (Renaud et al. 1990) may influence the synthesis and activity of substances of primary and secondary metabolites. Furthermore, coastal urbanization and its consequent anthropogenic pollution are renowned for causing declines in the diversity of biological communities (Juanes et al. 2008; Orfanidis et al. 2003; Scherner et al. 2013a). Martins et al. (2012) found that macroalgal communities from impacted areas of southern Brazil suffered a decrease in species richness and diversity, which was not observed in nearby pristine areas. We hypothesize that this loss of species richness leads to declines in the chemical profile of a given community whereas a wider range of substances derived from primary and secondary metabolism are expected in pristine areas.

Global warming, spreading low oxygen areas and acidification are environmental pressures that add to the stessors created by coastal habitat degradation (Gruber 2011; Hall-Spencer at al. 2008). These accelerating threats to coastal biodiversity reinforce the need for information about what we have now, what we are set to lose and what actions are needed to maintain the ecosystem goods and services upon which we rely (Halpern et al. 2008; Turra et al. 2013; Worm et al. 2006). In this paper we propose to evaluate the variety and abundance of primary and secondary metabolites produced by seaweeds on intertidal rocky shores as source of ecological information on both pristine and urbanized sites off the southern Brazilian coast. On the basis of chemical profiles we characterize, through simple and efficient tools, the damage caused by urbanization, including the loss of chemical compounds with potential biotechnological applications.

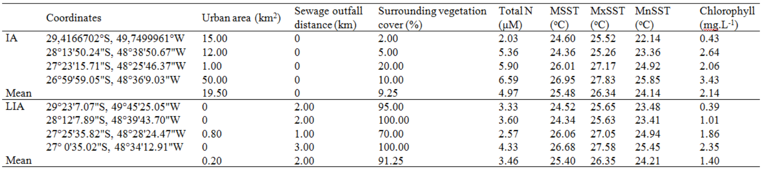
2. METHODS AND MATERIALS

2.1 Study Area and Sampling Design

Pairs of impacted (IA) and less impacted (LIA) areas were sampled in four municipalities in southern Brazil and some environmental factors evaluated as described in Martins et al. (2012). Besides these characteristics, the 4 km monthly summer value of sea surface temperature (SST) and chlorophyll a concentration was extracted from MODIS Aqua Ocean Level-3 standard mapped archive products (Feldman and McClain 2012), from 2003 to 2013, that are produced and distributed by the NASA Goddard Space Flight Center's Ocean Data Processing System (ODPS). The impacted areas were more urban and had lower water quality than the less impacted areas due to terrestrial run-off, sewage inputs, nutrient loading. Despite the temperature differences observed in the latitudinal gradient represented in the sampling region (southern areas are cooler than northern ones), LIA and IA presented similar values of this parameter (Table 1).

Samples were collected from Prainha (29°20'20"S, 49°43'57"W) (IA) and Guarita (29°21'63"S, 49°44'98"W) (LIA) in Torres County; Porto (28°13'86"S, 48° 39'01"W) (IA) and d'Água (28°12'00"S, 48°39'47"W) (LIA) in Imbituba County; Lagoinha de Ponta das Canas (27°23'67"S, 48°25'79"W) (IA) and Canajure (27°25'29"S, 48°28'40"W) (LIA) in Florianopolis County and Central (26°58'19"S, 48°37'75"W) (IA) and Taquarinhas (26°59'24"S, 48°34'89"W) (LIA) in Balneario Camboriu County (Figure 1). Sampling was conducted from February 10th to March 31st 2010, along three rocky shores on low spring tides. For chemical evaluation, in each shore seaweeds were removed scraped off the upper faces of horizontal rocks within 15 haphazardly placed quadrats (10 x 10cm) places on the characteristic seaweed community present in lower intertidal areas. The samples were placed in seawater and manually cleaned to remove epifauna, then dried at room temperature, macerated with liquid nitrogen and weighed. For community structure evaluation, 15 photoquadrats were taken from the same areas utilized to the chemical evaluation, as described by Martins et al. (2012).

Table 1: Land use of urbanized or Impacted (IA) and preserved or Less Impacted (LIA) beaches in the coastal plain of southern Brazil. Urban area, Sewage outfall distance and Surrounding vegetation cover were estimated based on satellite images. Total Nitrogen (Ammonia and Nitrate amount) was characterized as described by Martins et al. (2012). Chlorophyll and temperature (sea surface mean (MSST), Maximum (MxSST) and minimum (MnSST) are averages of monthly data during the summer season of the last 10 years (2003-2013).



	Coordinates	Urban area (km^2)	Sewage outfall distance (km)	Surrounding vegetation cover (%)	Total N (µM)	MSST (°C)	MxSST (°C)	MnSST (°C)	Chlorophyll (mg.L^{-1})
IA	29,4166702°S, 49,7499961°W	15.00	0	2.00	2.03	24.60	25.52	22.14	0.43
	28°13'50.24"S, 48°38'50.67"W	12.00	0	5.00	5.36	24.36	25.26	23.36	2.64
	27°23'15.71"S, 48°25'46.37"W	1.00	0	20.00	5.90	26.01	27.17	24.92	2.06
	26°59'59.05"S, 48°36'9.03"W	50.00	0	10.00	6.59	26.95	27.83	25.85	3.43
Mean		19.50	0	9.25	4.97	25.48	26.34	24.14	2.14
LIA	29°23'7.07"S, 49°45'25.05"W	0	2.00	95.00	3.33	24.52	25.65	23.48	0.39
	28°12'7.89"S, 48°39'43.70"W	0	2.00	100.00	3.60	24.34	25.63	23.41	1.01
	27°25'35.82"S, 48°28'24.47"W	0.80	1.00	70.00	2.57	26.06	27.05	24.94	1.86
	27° 0'35.02"S, 48°34'12.91"W	0	3.00	100.00	4.33	26.68	27.58	25.45	2.35
Mean		0.20	2.00	91.25	3.46	25.40	26.35	24.21	1.40

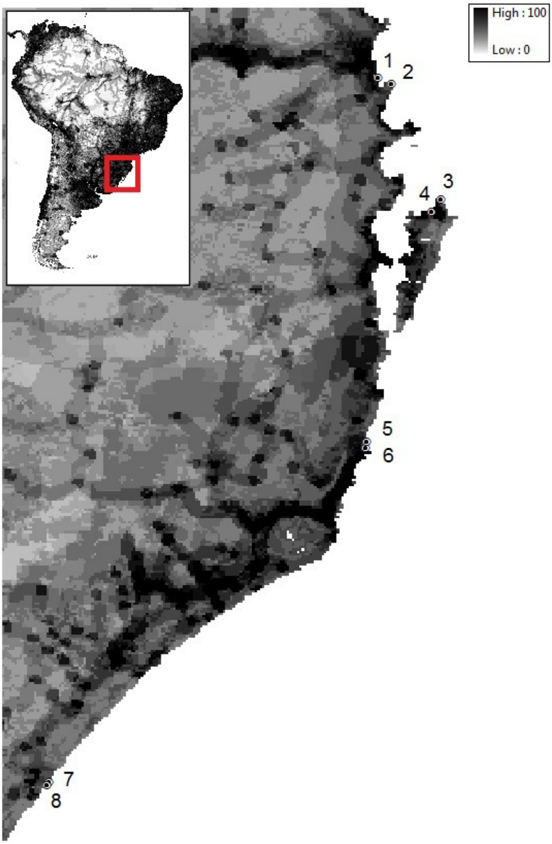


Figure 1: Study area map modified from Martins et al. (2012) showing all impacted and less impacted rocky shores sampled. The gray scale represents the relative density of human occupation.

2.2 Sample preparation and chemical profiles

A ratio of 1 ml of solvent for 1 mg of dry seaweed was used. To obtain the crude extract, a combination of organic solvents (v/v) was added to samples, starting with methyl alcohol 100%, methyl alcohol: dichloromethane (1:1) and dichloromethane 100%. The material was stored in a dry place, protected from light, and extracted for two days under each combination of solvents, under exhaust ventilation and a temperature of 25 (±2)°C. The organic extract was recovered by filtration through a cellulose support and this was analysed by thin layer chromatography assay (Wylie and Paul, 1988). The extracts were diluted with methyl alcohol to a concentration of 5mg.ml^{-1}; 50 µL of this dilution were applied for TLC revealed with ninhydrin (50%) for amino acids, sulfuric orcinol (0.25%) for lipids and sulfuricanisaldehyde (2%) for saponins, polyacetylenes and terpenoids. Chlorophyll and carotenoids were detected by visual inspection of thechromatoplates.

For qualitative analysis, we calculated the retention factors (rf) of each band within the same chemical class, such that each rf represented a taxon, or operational taxonomic unit (OTU), commonly employed in descriptive ecology (Blaxter et al., 2005; Hill et al., 2003). The present study utilized Chemical Operational Units (COUs) as a synonym for rf. To perform the quantitative analyses, the thin layer plates were analysed using QuantiScan software (Biosoft), which determined the amounts of the compounds in the samples , which are related to the densitometry of the spots (in cm^2) from each chemical class. The TLC-densitometry is a rapid and accurate method for quantitative determination that has been applied in different areas of science (Nikolova et al. 2004; Thennarasan et al. 2014; Vrancheva et al. 2012).

2.3 Data analysis

To verify differences between the chemical classes of samples from IA and LIA sites, tests of variance (ANOVA), available in STATISTICA 7.0, were employed. Homogeneity of variances was previously tested according to Levene's test. Chemoecological synthetic descriptors were applied to this work to calculate chemical richness (s), as determined by the number of COUs observed in each chemical class; abundance (n), as obtained from the area (in cm^2) occupied by bands present in each chemical class; and Shannon-Wiener diversity (H'), as calculated by the number of COUs and the area occupied by bands. We performed analysis of variance (ANOVA), using STATISTICA 7.0 package, to verify the differences between synthetic descriptors of IA and LIA environments.

In order to demonstrate the relationship between both biological (community structure) and chemical descriptors, as recommended by Wold et al. (1987), was performed a multivariate approach (Principal Component Analyses - PCA), considering all available information. Euclidian distance was based on log (x+1) transformed data and were visualized in a biplot analyses. Permutational multivariate analysis of variance (PERMANOVA) were used to evaluate the significance of ecological and chemical descriptors patterns between urbanized or Impacted areas and preserved or

Low Impacted Areas. All multivariate analyses were performed with the PRIMER 6.0 plus (Anderson et al. 2008).

3. RESULTS

There was a greater variety of Chemical Operational Units in the chlorophyll/ carotenoid group (F=8.09, p=0.005), in lipids (F=27.95, p <0.001) and in the terpenoid/polyacetylene group (F=10.47, p=0.001) in samples from LIA, compared to IA. In contrast, IA accounted for more COUs within the amino acid group (F=7.51, p = 0.007). Saponins data did not show homogeneity of variances according to Levene's test.

Quantitative analysis also showed significantly more chlorophylls/ carotenoids (F=7.88, p=0.005), lipids (F=17.33, p <0.001) and terpenoids/polyacetylenes (F=24.26, p<0.001) in the less impacted areas than in the impacted areas. We did not find significant differences in amino acids (F = 1.07, p > 0.05) and saponins (F = 2.95, p > 0.05) for the study areas (Table 2).

Table 2: List of COUs and their respective quantitative data (in cm^2) followed by standard error, for phytobenthic communities from less impacted (LIA) and impacted (IA) areas.

Chemical Classes		Torres		Imbituba		Florianópolis		Balneário Camboriu	
	COUs	LIA	IA	LIA	IA	LIA	IA	LIA	IA
Aminoacids	01	3951.49	5116.52	-	2897.58	-	1630.64	2591.03	1515.13
	02	3556.68	2737.07	361.93	1753.25	629.86	1397.12	2480.56	1325.81
	03	-	-	358.54	-	-	-	-	-
	04	2596.01	1998.89	-	1677.32	114.93	1123.57	1316.90	776.24
	05	3710.16	1357.57	-	1269.11	380.96	1182.84	1216.69	1224.86
	06	427.00	-	-	-	-	-	-	-
	07	441.08	-	-	-	2929.30	1885.19	-	-
Chlorophylls and Carotenoids	01	-	-	67.58	-	314.82	-	-	-
	02	-	-	192.60	-	546.81	-	-	-
	03	-	-	-	-	-	-	632.27	731.62
	04	-	222.68	200.61	-	1467.81	-	-	-
	05	194.19	559.38	221.69	-	383.51	-	2225.29	1301.59
	06	-	-	-	-	1196.39	-	-	-
	07	1773.26	1435.73	1065.18	1276.88	2695.91	-	2851.13	1432.24
	08	-	-	282.02	-	-	-	-	-
	09	1547.29	976.52	538.98	840.04	1364.72	2774.62	1156.62	-
	10	-	-	-	-	-	-	176.37	-
Lipids	01	3932.64	2654.89	2187.43	4744.64	814.57	1175.34	2235.87	336.01
	02	-	-	2230.41	2386.31	1006.20	-	-	-
	03	-	-	2282.10	-	669.57	948.30	2418.30	2181.91
	04	-	-	-	298.21	-	-	2108.92	-
	05	-	321.01	-	-	819.19	887.69	-	-
	06	-	-	3135.60	-	-	-	1055.43	1944.24
	07	-	-	4168.16	-	1546.34	1469.60	3253.61	1384.52
	08	506.19	861.28	-	232.02	-	-	-	1779.45
	09	308.80	806.83	3488.91	-	-	-	-	1883.64
	10	412.21	1013.02	2717.26	-	-	-	-	-
	11	711.46	813.35	-	972.41	1621.44	2408.18	-	-

	12	840.18	745.53	-	-	1528.91	2104.70	2638.94	-
	13	1302.75	236.51	-	-	94.90	1451.05	904.35	-
Saponins	01	1461.84	2244.05	354.35	1416.01	426.00	939.36	1086.61	2209.23
	02	1137.49	1737.98	225.44	1163.40	-	158.99	569.30	-
	03	-	-	-	-	84.46	-	-	-
	04	331.93	1101.83	724.06	553.64	554.84	295.36	835.63	2403.33
	05	-	-	-	-	140.20	-	-	449.82
	06	-	-	-	-	170.90	-	-	-
	07	687.36	1451.44	1555.98	1658.90	1333.37	1478.66	990.30	1243.77
	08	301.28	1764.85	2180.22	1933.89	1566.68	534.84	1076.36	136.19
	09	269.09	260.79	1936.98	2543.92	1400.08	780.20	1291.13	665.35
	10	789.92	424.52	2558.07	1487.61	2052.15	965.42	1777.76	867.72
	11	83.06	-	2169.10	373.98	998.10	789.22	1214.96	500.22
	12	1602.58	794.11	3227.00	2054.47	3128.35	2156.34	1514.37	-
	13	-	-	1756.78	225.93	442.98	-	1404.64	945.24
Terpenoids	01	993.48	1398.89	4789.15	2598.33	6176.97	3313.74	3255.77	187.86
	02	334.65	797.37	1216.00	-	3683.94	2293.81	1676.68	-
	03	-	61.27	1637.10	542.93	-	218.90	-	-
	04	-	-	-	-	-	830.79	-	-
	05	-	-	-	-	-	-	-	-
	06	-	-	2946.64	262.34	-	222.59	-	-
	07	-	623.48	-	-	-	251.59	-	-
	08	-	-	-	-	2150.05	705.61	-	-
	09	-	-	2537.13	3264.41	6018.52	4979.48	-	-

The chemical richness, abundance and diversity was clearly higher in samples from less impacted areas (16.65±1.14; 45981±3501.3; 2.61±0.08, respectively) than in impacted areas (12.68±1.05; 35431±3663.07; 2.35±0.11, respectively) throughout southern Brazil (Figure 2).

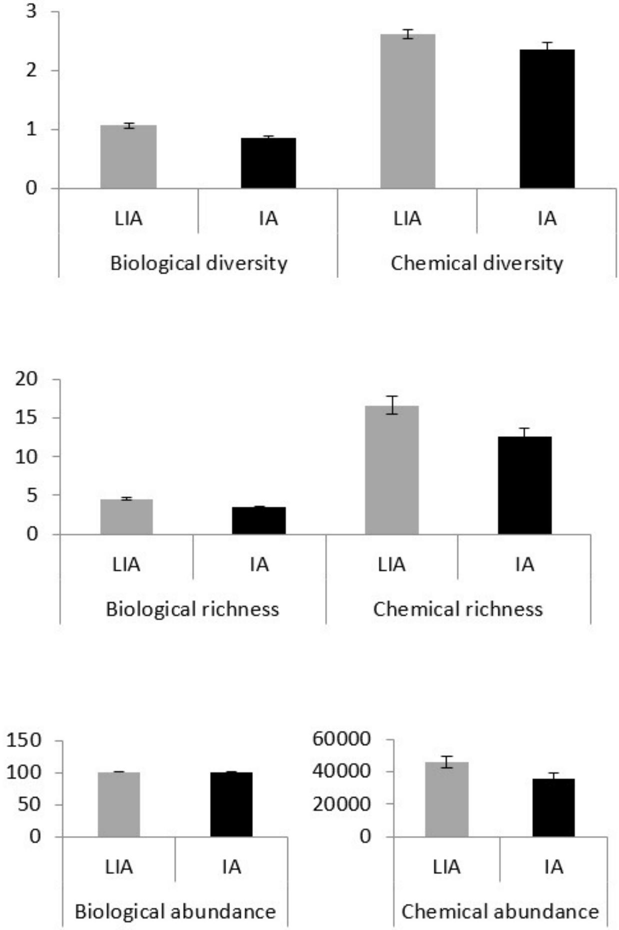


Figure 2: Mean and standard error (n=4) of biological (modified from Martins et al., 2012) and chemoecological synthetic descriptors: richness, Shannon-Wiener diversity and abundance for phytobenthic communities from less impacted (LIA) and impacted (IA) areas.

The data yielded 4 principal components (PCs) that explained more than 50% of the total variability (Fig. 3). The first two PC explained approximately 27 % of the total variation. The first PC has positive correlation with surrounding vegetation cover, sewage outfall distance, occurrence of saponins, chlorophyll, lipids and terpenes and the higher abundances of *Sargassum* spp., *Gelidium* spp., *Centroceras* spp., *Chaetomorpha* spp. and *Hypnea* spp. This axis has negative loadings on percentage of urban area cover, total N, water surface chlorophyll and the occurrence of amino acids and the genus *Ulva* spp. This component was called land cover, which reinforce the correlation between that the urbanization processes, with soil sealing and the reduction of surrounding vegetation cover, and the impoverishment of the phytobenthic community structure and chemical composition of their constituent organisms. Furthermore, terpenes seem to be positively correlated with this axis and therefore with less impacted areas. Despite the other three main axis be related with, respectively, temperature changes observed within the sampling region and heterogeneities of each site, as those produced by topographic and hydrodynamics changes, the pattern observed in the parametric approach is corroborated with the multivariate approach. PERMANOVA highlight the significance of differences produced by the urban impacts ($p<0,05$), considering the community structure and chemical descriptors, isolated or in the same analyses, as illustrated in the Fig. 3.

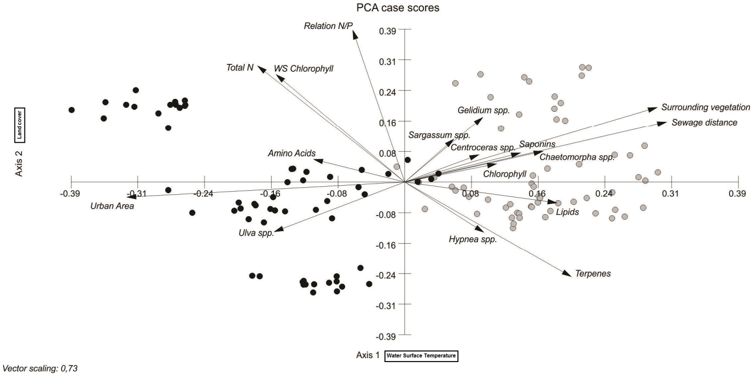


Figure 3: Biplots of the principal components analysis (PCA) for phytobenthic community structure and chemical diversity from less impacted (gray) and impacted areas (bold).

4. DISCUSSION

Few authors have investigated the effects of urbanization on processes related to production and diversity of metabolites in seaweed communities. The literature provides evidence of the effects of single stressors, such as ultraviolet radiation, temperature and heavy metal contamination in seawater, on the production of secondary metabolites in specific populations (Amade andLemée, 1998; Fairhead et al., 2006; Pavia et al., 1997; Pavia and Brock, 2000; Toth and Pavia, 2000). For a holistic overview, we need to understand how factors that are known to cause changes in metabolite production combine with stressors, such as continental runoff and domestic sewage pollution, to alter the chemical composition of coastal marine communities. The rapid urbanization of Latin America coastlines provides insights into how altered light availability and pollutant concentrations may have affected coastal habitats that were urbanized long ago (Martins et al., 2012).

We found consistent significant reductions in the diversity and abundance of a suite of chemical compounds synthesized by phytobenthic communities when we compared coastlines within protected areas with those impacted by urbanization, both in the parametric and non-parametric analyses. The fall in richness and abundance of chlorophylls and carotenoids correlates with increases in the water turbidity due effluent discharge with high concentrations of dissolved organic and inorganic matter (Davies-Colley and Smith, 2001). This seaweed chlorophyll reduction mirrors the reduction in phytoplankton primary production recorded globally, but especially important in coastal areas near urbanized environments (Boyce et al., 2010). The toxic effect of ammonia observed at our urbanized study sites (Martins et al., 2012), may also impair metabolite synthesis (Ogawa, 1984), causing the observed reduction of these chemicals on coasts impacted by urbanization, as reinforced by PCA.

The qualitative and quantitative reduction of lipid compounds may be related to the reduction in physiological performance of species able to survive on urban shores. The combined environmental stressors in urban areas can cause physiological deterioration in seaweeds, reducing growth and community diversity (Dolbeth et al., 2007). It is noteworthy that there were more amino acids found in seaweeds collected at the impacted areas since 1) stress can trigger cellular repair processes that lead to amino acid synthesis and 2) urbanized environments have more dissolved nitrogen which may limit algal protein synthesis in oligotrophic waters (Lobban and Harison, 1997).

The richness, abundance and diversity of chemicals were consistently higher in samples from less impacted beaches when compared to samples from impacted beaches of the same municipality. Martins et al. (2012) found higher seaweed species richness and Shannon–Wiener diversity in the less impacted areas (4.54 ± 0.18 and 1.06 ± 0.04, respectively) in relation to urbanized ones (3.50 ± 0.15 and 0.85 ± 0.04, respectively). These authors showed that at our urbanized study sites the beaches had >60% cover of *Ulva* spp. whereas marine protected areas had only 30% cover these green algae which are known to proliferate in environments with high nutrient concentrations or near sewage discharges (Littler and Murray, 1975; Merrill and Fletcher, 1991; Soltan et al., 2001). The seaweed biodiversity data of Martins et al. (2012) correlates with our seaweed chemical diversity dataset; a larger number of species, with potentially better physiological performance, results in an environment with greater diversity of chemical compounds. Here we show that marine protected areas can enhance the biodiversity of seaweeds and preserve a wider range of primary and secondary metabolites which may have biotechnological potential.

The consequences of reducing the richness and abundance of primary and secondary seaweeds metabolites will ramify through food webs potentially affecting fish stocks and food security. Santos et al. (2009) noted that *Chelonia mydas* turtles that inhabit urbanized environments had more skin tumors, than those feeding in more pristine environments. These authors attribute immunedeficiency in these animals to low nutritional quality provided by flora from degraded environments. The increase in the diversity and abundance of carotenoids that we observed within protected areas of coastline could strengthen the immune system of potential consumers as they are well known antioxidants. Our observed losses of chemical diversity represent degradation in the social and economic value of these environments (Barbier et al., 2008).

We recommend that efforts be made to create indices that can pinpoint the advantages gained by marine protection and improved coastal management, including the enhancement of chemical heterogeneity in ecosystems and their biotechnological potential. Knowledge of the impact of pollution on the structure of algae-dominated communities goes back several decades (Ballesteros et al., 2007) and the scientific community have no doubt that the marine environments are losing quickly biodiversity. However, in this paper, we propose the evaluation of additional perspective of these impacts, the seaweed chemical richness and abundance. This metabolic perspective, represent a simple and powerful tool to evaluate the conservation status of coastal environments, once the observed chemical patterns were unique to conditions of LIA or IA. Our results represent an important example in science when applied phycology meets traditional fields, as benthic ecology. These patterns represent strong arguments to increment coastal management discussions, improving conservation importance of high diversity areas, also suggesting the biotechnological potential these environments and organisms.

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Table S1: List of species and their functional group classification ("FL" for filamentous, "CO" for corticated terete and "CA" for calcareous articulated) sampled at Fernando de Noronha (FN), Atol das Rocas (RO), Natal (RN), Tamandaré (PE), Maragogi (AL), Salvador (BA), Guarapari (ES), Arraial do Cabo (RJ), Ilhabela (SP) and Florianópolis (SC), which were aggregated into 3 regions: extreme tropical (ET), tropical (TR) and warm temperate (WT). Total biomass is shown as mg per 0.01 m^2.

		ET			TR				WT		
		FN	RO	RN	PE	AL	BA	ES	RJ	SP	SC
Rhodophyta											
Acrochaetium sp. Nägeli	FL	0.01	0.001	0	0	0	0	0	0.06	0	0
Aglaothamnion sp. Feldmann-Mazoyer	FL	0	0	0.001	0	0	0	0	0	0	0
Aglaothamnion felipponei (Howe) Aponte. Ballantine & J.N.Norris	FL	0	0	0	0.003	0	0	0	0	0	0
Amphiroa sp. J. V. Lamouroux	CA	3.86	62.08	1.63	552.27	409.36	0	101.00	322.80	63.04	47.63
Anotrichium tenue (Okamura) Baldock	FL	0	0	0	0	0	0	0	0.01	0	0
Anotrichium yagii (Okamura) Baldock	FL	0	0	0	0	0	0	0	0	0	0.02
Asparagopsis taxiformis (Delile) Trevisan de Saint-Léon	FL	0	0	0	0	0	0	0	0.02	2.73	0.06
Botryocladia occidentalis (Børgesen) Kylin	CO	0	0	0.01	0	0	0	0	0	0	0
Bryothamnion triquetrum (S.G.Gmelin) M.A.Howe	CO	0	0.14	0	0	0	0	0	0	0	0
Centroceras sp. Kützing	FL	0.001	0	0	0	0	0	0.003	0.004	0.28	0
Centroceras clavulatum (C. Agardh) Montagne	FL	2.70	0	0	0	0	0	0	6.59	0	0.001
Ceramium sp. Roth	FL	0.11	0.001	0.001	0	0.002	0	0	0.41	0.33	0
Ceramium comptum Børgesen	FL	0	0	0	0	0	0	0	0.01	0	0
Ceramium dawsonii A. B. Joly	FL	0	0	0	0	0.001	0	0	0	0	0
Ceramium diaphanum (Lightfoot) Roth	FL	0	0	0	0	0	0	0	0.01	0	0
Ceramium tenerrimum (G. Martens) Okamura	FL	0	0	0	0	0.001	0	0	0.01	0	0
Champia sp. Desvaux. 1809	CO	0.001	0	0	0	0.09	0	0.07	0	0.14	0
Champia minuscula A. B. Joly & Ugadim	CO	0	0	0	0	0.16	0	0	0.16	0	0.04
Ceratodictyon variabile (J. Agardh) R. E. Norris	CO	0	0	0	0	0	0	0	0	0	1.19
Cheilosporum sp. (Decaisne) Zanardini	CA	0	0	0	0	0	0	0.99	0	0	0
Chondracanthus acicularis (Roth) Fredericq	CO	0	0	0	0	0	0	4.97	3.10	3.74	0.05
Chondria polyrhiza F. S. Collins & Hervey	CO	0	65.51	0	0	0	0	0	0	0	0
Chondria sp. C. Agardh	CO	0	0.01	0	0	0.06	0	0	0.03	0	0
Digenea simplex (Wulfen) C. Agardh	CO	0	42.63	0	0	7.01	0	0	0	0	0
Erythrocladia sp. Rosenvinge	FL	0	0.001	0	0	0	0	0	0	0	0
Erythrotrichia sp. Areschoug	FL	0	0.001	0	0	0	0	0	0.08	0	0.02
Gelidiella acerosa (Forsskål) Feldmann & G. Hamel	CO	0	2.89	0	34.13	8.84	0	1.51	0	0.04	0
Gelidiella sp. Feldmann & G.Hamel	CO	0	0.52	0.56	0	0	0	0	0	0	0
Gelidiopsis sp. F. Schmitz	CO	0	0	0.06	0	0	0	0	0	0	0
Gelidium americanum (W. R. Taylor) Santelices	CO	0	0.004	0	0	0	0	0	0	0	0
Gelidium crinale (Hare ex Turner) Gaillon	CO	0.59	11.18	4.09	18.21	11.91	26.70	8.20	5.23	1.24	1.15
Gelidium floridanum W. R. Taylor	CO	0	0	1.51	17.40	14.00	0	5.53	0	0	0.01
Gelidium pusillum (Stackhouse) Le Jolis	CO	0.01	1.58	1.21	0.11	3.11	0.18	14.54	0.09	0.19	0
Gelidium sp. J. V. Lamouroux	CO	1.25	0.01	0	0.001	0	0.69	0	0	0	0
Herposiphonia sp. Nägeli	FL	0	0	0	0	0.001	0	0	0.06	0	0
Herposiphonia secunda (C. Agardh) Ambronn	FL	0	0	0.01	0	0	0	0	0	0	0
Heterosiphonia sp. Montagne	FL	0	0	0	0	0.001	0	0	0.01	0	0
Heterosiphonia crispella (C. Agardh) M. J. Wynne	FL	0	0	0.001	0	0.001	0	0	0.004	0	0
Hypnea spinella (C. Agardh) Kützing	CO	0	0.66	0.33	9.17	24.82	0	0	9.83	0.56	0.78
Hypnea musciformis (Wulfen) J. V. Lamouroux	CO	0.001	0.19	0	3.17	1.06	0	0	0	4.41	0
Hypnea volubilis Searles	CO	0	0	0	0	0	0	0	0.03	0	0
Hypoglossum hypoglossoides (Stackhouse) F.S. Collins & Hervey	CO	0	0	0	0	0	0	0	0.08	0	0
Jania sp. J. V. Lamouroux	CA	0	62.08	0.16	552.27	1.09	0	0	20.90	63.04	29.25
Jania adhaerens J. V. Lamouroux	CA	0	61.21	0	0	360.40	0	0	0	0	0
Jania capillacea Harvey	CA	0	38.98	0	0	0	0	0	0	0	0
Jania subulata (Ellis & Solander) Sonder	CA	0	0.001	0	0	0	0	0	0	0	0
Jania verrucosa J. V. Lamouroux	CA	0	6	0	0	0	0	0	0	0	0
Jania prolifera A. B. Joly	CA	0	0.04	2.72	181.29	45.64	0.22	43.38	0	86.92	0
Laurencia sp. J. V. Lamouroux	CO	0.20	0	0.32	0	3.25	0	0	0	0.02	0
Laurencia oliveirana Yoneshigue	CO	0	0	0.01	0	0	0	0	0	0	0
Lomentaria corallicola Børgesen	CO	0	0	0	0	0	0	0	0.02	0	0.001
Neosiphonia sp. M.-S.Kim & I.K.Lee	FL	0	0	0	0	0	0	0.003	0	0	0
Neosiphonia ferulacea (Suhr ex J. Agardh) S.M.Guimarães & M.T.Fujii	FL	0	0	0	0	0	0	2.97	0.01	0	0

Nitophyllum adhaerens M. J. Wynne	CO	0	0	0	0	0	0	0	0.01	0	0
Peyssonnelia sp. Decaisne	CO	0	0	0	0	0	0	0	2.28	0	0
Plocamium brasiliense (Greville) M. A. Howe & W. R. Taylor	FL	0	0	0	0	0	0	0	0.66	0.21	0
Polysiphonia sp. Greville	FL	1.15	0.001	0.001	0	0.001	0	0	0.01	1.07	0
Polysiphonia decussata Hollenberg	FL	0	0	0	0	0.001	0	0	0	0	0
Polysiphonia howei Hollenberg	FL	0	0	0	0	0.001	0	0	0	0	0
Polysiphonia subtilissima Montagne	FL	0	0.001	0	0	0	0	0	0	0	0
Pterocladiella sanctarum (Feldmann & Hamel) Santelices	CO	0	0.28	0	0	0	0	0	0	0	0
Spyridia hypnoides (Bory de Saint-Vincent) Papenfuss	FL	0	0	0	0	0	0	0	1.94	0	0
Stylonema alsidii (Zanardini) K. M. Drew	FL	0	0	0	0	0	0	0	0.01	0	0
Wrangelia argus (Montagne) Montagne	FL	0	0	1.34	0	0	0	0	0	0	0
Chlorophyta											
Bryopsis sp. J. V. Lamouroux	FL	0	0.001	0	0	0	0	0	0	0	0
Bryopsis pennata J. V. Lamouroux	FL	0	0	0	0	0	0	0	0.003	0	0.001
Bryopsis plumosa (Hudson) C. Agardh	FL	0	0	0	0	0	0	0	0	0	0.001
Caulerpa sp. J. V. Lamouroux	CO	0	0	0	6.41	0.02	0	0.003	0.001	0	0
Caulerpa fastigiata Montagne	CO	0	0	0	0	0.001	0	0	0	0	0
Caulerpa mexicana Sonder ex Kützing	CO	0	0.88	0	0	0	0	0	0	0	0
Caulerpa verticillata J. Agardh	CO	0	0.12	0.18	0	0	0	0	0	0	0
Caulerpella ambigua (Okamura) Prud'homme van Reine & Lokhorst	CO	0	1.28	0.001	0	0	0	0	0.58	0.02	0
Chaetomorpha spiralis Okamura	CO	0	0.08	0	0	0	0	0	0	0	0
Cladophora sp. Kützing	FL	0.11	2.77	0	0.001	0.10	0.70	0.41	0.01	0.62	0.03
Cladophora vagabunda (Linnaeus) Hoek	FL	0	0	0	0	0	0	0	0.01	0.10	0
Cladophoropsis sp. Børgesen	FL	0	0	0	0	0	0	0	0	0	0.11
Codium sp. Stackhouse	CO	0	0	0	0	0	0	0	0	0.13	0
Derbesia marina (Lyngbye) Solier	FL	0.19	0.28	0	0	0	0	0	11.11	0	0
Halimeda sp. J. V. Lamouroux	CA	0	0	0	100.07	104.73	0	0	0	0	0
Microdictyon sp. Decaisne	CO	0	0	0	0	0	0	0	0.50	0	0
Ulva sp. Linnaeus	CO	0	0	0	0	0	0.73	0	0.03	0.18	0
Ulva flexuosa Wulfen	CO	0	0	0	0	0	0	0	0.09	0.03	0
Valonia sp. C. Agardh	CO	0	3.05	0	0	0.001	0	0	0	0.44	0
Phaeophycea											
Canistrocarpus cervicornis (Kützing) De Paula & De Clerck	CO	4.63	1.86	40.76	0	1.67	0.33	11.42	0.45	0.29	3.20
Canistrocarpus crispatus (J. V. Lamouroux) De Paula & De Clerck	CO	0	0	6.02	0	0	0	0	3.18	0	0
Dictyopteris delicatula J. V. Lamouroux	CO	0	5.9	11.94	1.44	0	0	0	0	0	0
Dictyopteris justii J.V.Lamouroux	CO	0	0	0.44	0	0	0	0	0.01	0	0
Dictyopteris plagiogramma (Montagne) Vickers	CO	0	0.33	0	0	0	0	0	0	0	0
Dictyopteris sp. J.V.Lamouroux	CO	0.09	0.66	0.37	0	0.001	0	0.03	0	0.11	0
Dictyota sp. J. V. Lamouroux	CO	0	0	0	0.06	0	0	9.55	0	0	0
Dictyota mertensii (Martius) Kützing	CO	0	0.38	0	0	0	0	0	0	0	0
Dictyota pulchella Hörnig & Schnetter	CO	0	1.5	0.03	0.15	0	0	0	0	0	0
Ectocarpus sp. Lyngbye	FL	0	0.05	0	0	0	0	0	0	0	0
Feldmannia mitchelliae (Harvey) H.-S.Kim	FL	0	0	0	0	0	0	0	0	0.001	0
Levringia sp. Kylin	CO	0	8.48	0	0	0	0	0	0	0	0
Lobophora variegata (J. V. Lamouroux) Womersley ex E. C.Oliveira	CO	0.11	0	0	0	0	0	0	0	0	0
Lobophora sp. J. Agardh	CO	0	0.58	0	0	0	0	0	0	0.06	0.27
Padina sp. Adanson	CO	0.02	0.01	0	0	0.08	0	0	0	0.14	0.58
Sargassum sp. C. Agardh	CO	0	0.16	0.02	0	0	0	1.62	0	5.42	10.63
Sphacelaria sp. Lyngbye	FL	4.18	0.67	0.001	0	0	0	0.68	8.49	0	0
Sphacelaria rigidula Kützing	FL	0	0	0	0	0	0	0	0	0	0.001
Sphacelaria tribuloides Meneghini	FL	0	0	0	0	0	0	0	0	0.001	0

CAPÍTULO 2

Macroecological drivers of algal turf assemblages of the Southwestern Atlantic

(Em revisão no periódico *Marine Ecology Progress Series*)
Formatação de acordo com as exigências da revista

MARTINS, C.D.L.; LONGO, G.O.; AUED, A.W.; SISSINI, M.N.; GIEHL, E.L.H.; LUCENA, L.A.F.; SCHMITZ, C.; FERREIRA, C.E.L.; FLOETER, S.R.; HORTA, P.A. (*no prelo*) Macroecological drivers of algal turf assemblages of the Southwestern Atlantic.

MACROECOLOGICAL DRIVERS OF ALGAL TURF ASSEMBLAGES OF THE SOUTHWESTERN ATLANTIC

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ABSTRACT

Turf algae assemblages are among the main constituents of tropical and warm temperate benthic communities. Despite such broad distribution, the macroecological drivers of local and regional turf algae composition are still poorly understood. Herein we described the composition and abundance of turf assemblages from coastal and oceanic reefs across a latitudinal gradient of 4000 Km of coastline in the southwestern Atlantic and assessed the role of potential drivers of distribution across regional and local scales. We recorded 102 taxa of macroalgae across all turf assemblages. Nine species, all belonging to calcareous articulated algae, made up 83% of the total biomass of all sampled sites. This supports the assumption that minimum and maximum sea surface temperature (SST) isotherms may be important for determining the composition of macroalgae assemblages. Turf biomass was greater in the tropical region and correlated positively with high photosynthetically active radiation and SST values. The most plausible explanation for this pattern of abundance combines ecophysiological behavior with biotic interactions, as the dominant species utilize physical or chemical strategies to avoid herbivory, which is potentially higher in tropical environments. Herbivory, traditionally regarded as a local ecological factor, coupled with temperature and irradiance, seem to be key drivers of turf composition and community structure.

Key Words: Epilithic algal matrix, Latitudinal pattern, Richness, Abundance

1. INTRODUCTION

Biodiversity-based experimental or observational research has among their main challenges scaling-up efforts (Naeem 2006). Expanding scales demand enhanced number and quality of robust characterization of natural processes that will contribute to our understanding about evolutionary and macroecological drivers that shape ecological or biogeographical patterns (Evans et al. 2005). This acknowledgement sustains arguments such as those related with the proposition of Large Marine Ecosystems (LME), which are utilized to foster coastal management and conservation initiatives (Spalding et al. 2007). However, identification of these environmental drivers that construct the community composition and structure of different ecosystems in regional scales is still missing.

Patterns of distribution are among the main debated topics in terms of causal factors and ecological drivers. Despite the classic global diversity gradient of high species richness in low latitudes (Willig et al. 2003, Hillebrand 2004), for many marine groups, such as macroalgae, mid-latitude areas present peaks of species richness (Chaudhary et al. 2016). The role of bottom-up and top-down stressors influencing the composition and structure of benthic communities demand more arguments and further discussions.

Sea temperature (ST) is an important macroecological driver, recognized as a predictor of global distribution of macroalgae and as the main abiotic factor that directly relates to geographic boundaries of macroalgae species. Many marine plants can tolerate variable sea temperature, and cooling or heating will influence life cycle, reproduction, and processes related with settlement and development(Van Den Hoek 1982, Lüning 1990, De Faveri 2015).Moreover, dissolved inorganic nutrients (DINs), which often times are influenced by local drivers (Scherner at al. 2012, 2013, De Faveri 2015), also determine distribution on a global scale. Nitrogen and phosphate can regulate macroalgae survival, growth, and reproduction (Steneck et al. 2002, Gordillo 2012). Rivers and upwelling zones represent sources of these nutrients, but extreme concentrations can limit macroalgal development (Gao et al. 2012; Tait & Schiel 2013), reducing richness (Kautsky et al. 1986, Borum & Sand-Jensen 1996, Martins et al. 2012).Along with irradiance, these three factors represent the main abiotic drivers responsible for structuring primary producer's assemblages in subtidal zones, driving occurrence and abundance of species. Photosynthetically active radiation (PAR), which is determined by radiation intensity, water transparency and depth, is a key limiting factor for macroalgae photosynthesis (Graham et al. 2009, Hanelt & Figueroa 2012, Martínez et al. 2012), and is listed among the main drivers of latitudinal or vertical gradients (Eggert 2012). PAR and sea temperature reach high values in lower latitudes. However, local anthropogenic activities can influence all these factors. Cities and power station effluents produce warmer plumes, as well as reducing PAR in the benthos related to water turbidity, or enhancing nutrient concentration caused by sewage release.

Nevertheless, differences in the structure of macroalgae communities may also result from variations in the kind and intensity of interspecific biological interactions occurring in different locations. At low latitudes, biological interactions, such as competition for substrate as well as herbivory pressure, are hypothesized to be relatively more important than physical/chemical drivers, influencing large-scale diversity gradients (Pianka 1966, Wiens & Donoghue 2004). On coral reefs, for example, it is well documented that disturbance by herbivores can control benthic algal community structure (Lewis & Wainwright 1985). Furthermore, biomass and species richness of herbivorous fishes tend to be higher in the tropics (Floeter et al. 2005), and grazing reduces the biomass of macroalgae (Burkepile & Hay 2008, Mumby 2009). Nevertheless, high herbivory alone does not prevent algal growth when nutrients, SST or PAR are high, and the opposite is also true. Another effect of anthropogenic activities on macroalgal communities occurs indirectly by selective or unselective fisheries. In the first case, suppression or even the local extinction of carnivorous species results in a cascade effect that locally increases herbivory rates. In the second case, suppression of fish stocks reduces total fish biomass, reducing herbivory and thus top-down regulation of macroalgal communities(Carpenter et al. 1985, Steneck 1998, Daskalov 2002).Consequently, we can state that the distribution and abundance of macroalgae communities are shaped through a combination of bottom-up control, mainly represented by temperature, irradiance and nutrient availability, and top-down control, which biologically reduces algal biomass (Littler et al. 2006).

Among macroalgal assemblage community structure, the apparently ephemeral turf algal are widespread and ecologically essential, whose importance have been increasingly recognized in regards to processes related to global changes (Harris et al. 2015).While canopy-forming species are organized on the scale of cm to m, populations that compose algal turf formations structure their assemblages in scales of mm to cm. Algae turfs are sparse- to thick mats of diminutive and juvenile algae less than 2 cm high and have major ecological functions, contributing up to 80% of primary production in reef environments (Adey & Steneck 1985) and fixing substantial amounts of nitrogen (Williams & Carpenter 1997, 1998. Algal turfs are the main feeding substratum for several reef organisms, especially herbivorous and detritivorous fish species (Wilson et al. 2003, Ferreira & Gonçalves 2006, Bonaldo & Bellwood 2008). Previous studies have demonstrated that algal turfs can have strong effects on the distribution of mesofaunal organisms that live in the turf matrix (Kelaher et al. 2001), providing protection from dislocation due to wave action and restricting the variability of temperature on the shore (Kelaher et al. 2001, Bulleri & Benedetti-Cecchi 2006). The habitat structure provided by turf can also act as a filter to larvae, swimming or drifting adults, and provide a refuge from predation by large mobile predators such as fishes (Coull & Wells 1983). Together, these components form an epilithic algal matrix (EAM), a ubiquitous feature of coral reefs, which often occupies more benthic space than corals and conspicuous macroalgae (Wismer et al. 2009). Compared with other benthic groups, turf-forming species grow faster (Littler et al. 2006), occupy vacant spaces more quickly (Airoldi 1998) and are less vulnerable to physical stress (Cheroske et al. 2000). This means that with increasing disturbance, algal biomass and canopy height would be reduced and shifted to fast-growing algal turfs (Littler et al. 1983, Steneck & Dethier 1994). Experimental approaches reveal that the impacts caused by synergistic effects of climate change (elevated carbon dioxide and subsequent ocean acidification) and elevated nutrients can interact with each other and increase the abundance of turf-forming algae. This highlights the importance of these assemblages in the future, under a scenario of acidified oceans combined with coastal pollution (Russel et al. 2009).

Algal turfs represent ubiquitous assemblages facilitating standardized evaluations of the benthic environment and discussion of macroecological drivers in a large-scale perspective. Considering the tropical and warm temperate affinities identified in the southwestern Atlantic coast (Horta et al. 2001), this region stands out as promising area to test the hypothesis that richness of primary producers is higher in intermediary values of temperature, combined with drivers influenced by local stressors such as PAR and DIN. We also expect that, as a dip in a fractal dimension of community structure, the biogeographical pattern described by entire community must be present in turf assemblages. Therefore, herein we describe the composition and structure of turf algal assemblages of the southwestern Atlantic considering a sampling effort representing more than 6,000 km of coast line.

2. METHODS AND MATERIALS

2.1 Study region and data collection

Algal turfs were sampled in 10 reef sites along 4000 Km of coast line in the southwestern Atlantic, from January 2012 to August 2013, through total scraping of 110 haphazardly placed quadrats (0.01 m^2 each) (Table 1). These sites were aggregated into 3 regions, based on the latitudinal proximity among them: three sites represented the extreme tropical region (ET), including two oceanic islands, four sites represented the tropical region (TR), while three represented the warm temperate region (WT). For sample collections, turf was defined as distinct mats of low-growing algae <5 cm canopy height. The coordinates from each sampling site were taken thereafter from GoogleEarth® (version 7.1.2.2041). Environmental factors were also evaluated from each site: (1) annual mean, minimum and maximum values of sea surface temperature (SST), (2) photosynthetically active radiation (PAR), (3) Chlorophyll *a*, (4) oxygen, (5) pH, (6) nitrate, (7) phosphate and (8) salinity were extracted from MODIS Aqua Ocean Level-3 standard mapped archive products (Feldman & McClain 2012), produced and distributed by the NASA Goddard Space Flight Center's Ocean Data Processing System (ODPS) (data from 2003 to 2013); (9) means, minimum and maximum depths of sampling were taken *in situ*; and (10) distance of each site from the coastline was calculated using satellite images taken from GoogleEarth®.

In laboratory, samples were washed with seawater to remove sand and epifauna from macroalgae thalli and with ammonium formiate to remove salts. Samples were examined using an Olympus CX31 binocular microscope to identify taxa to the lowest functional taxonomic level (usually species). All identified species belonging to the same sample were dried separately at 38°C (± 2°C) for 24 hours to determine dry weight through an analytical balance (model FA2104N, Bioprecisa).

2.2 Data analysis

For descriptive results, all identified species were classified within functional groups, according to Steneck and Dethier (1994). Three major groups of turf-forming algae were recognized: (1) “filamentous” (FL), including uniseriate, multiseriate, lightly corticated or polysiphonous filamentous algae; (2) “corticated terete” (CO), including branched, upright, extensively corticated, fleshy to wiry algae; and (3) “calcareous articulated” (CA), consisting of calcified, articulated algae. Although algae with other morphologies, such as foliose, generally represent < 5% of the turf cover, we also consider them in our work.

Initially the relationships between species richness and total biomass with potential explanatory variables were explored using bivariate plots. In both cases, mean SST, nitrate, PAR, mean depth, coastal distance and classification by three regions were considered as potential predictors. All other variables were removed after a preliminary round of analyses as they were redundant with the information contained in this subset of variables. Next, species richness and total biomass were modeled with generalized linear models (GLM). Species richness was best modeled using the Poisson distribution (against normal and negative binomial distribution) and total biomass using the Gamma distribution with logarithmic link function (against normal distribution). In each case, the set of candidate explanatory variables model simplification was carried out using Akaike Information Criterion (AIC).

To test for effects of environmental variables on species biomass and composition, we used a model-based approach. First, we modelled the species matrix solely based on site effects to be able to represent the main differences in biomass and composition between sites (pure latent variable model). This approach is known as model-based ordination and resulted in an ordination biplot scaled for both species and sites (Hui et al. 2015). We then assessed the importance of mean SST, nitrate, PAR, mean depth, coastal distance and classification in three regions as potential drivers of changes on species biomass and composition between sites with a correlated response GLM (Hui et al. 2015, Warton et al. 2015). Because of the number of environmental variables we assessed, we kept only species occurring in at least seven sites in this analysis. The biomass of each species was modelled as a function of the predictors, with site effects estimated as random. We tested the fit of such model using three distributions for species biomass: the log-normal, gamma and Tweedie distribution, with the Tweedie distribution showing a better fit to the data. Model parameters were fit using a Bayesian approach and highest posterior densities used to infer effects of environmental variables on the biomass of each species and were used to construct caterpillar plots. Pure latent variable model and correlated response GLM were calculated using the Boral package (Hui et al. 2015) in R 3.3.2 (R Core Team 2016).

3. RESULTS

The extreme tropical province was characterized by higher irradiance and water temperature (both minimum and maximum values), when compared to tropical and warm temperate regions. The sampling depths ranged from 1 to 18 meters among extreme tropical sites, from 1 to 16 meters among tropical and from 3 to 11 among warm temperate ones. The distances of sampling sites from the nearest point on the coastline were 7, 360 and 510 kilometers in the extreme tropical region, the last two corresponding to oceanic islands. Among tropical sites this distance ranged from 0 to 7 kilometers and among warm temperate sites it ranged from 0 to 4 kilometers (Table 1).

Table 1: Sites where samples were collected and their corresponding region ("ET" for extreme tropical, "TR" for tropical and "WT" for warm temperate) and abiotic parameters (1) annual means, minimum and maximum values of sea surface temperature (SST), (2) photosynthetically active radiation (PAR), (3) Chlorophyll *a*, (4) oxygen, (5) pH, (6) nitrate, (7) phosphate and (8) salinity were extracted from MODIS Aqua Ocean Level-3 standard mapped archive products (Feldman & McClain 2012), produced and distributed by the NASA Goddard Space Flight Center's Ocean Data Processing System (ODPS) (data from 2003 to 2013); (9) means, minimum and maximum depths of sampling were taken *in situ*; and (10) distance of each site from the coastline was calculated using satellite images taken from GoogleEarth®

Region	**Site**	**Coordinates**	**SST (mean)**	**SST (min)**	**SST (max)**	**PAR**	**Chlorophyll *a***	**Oxygen**	**pH**	**Nitrate**	**Phosphate**	**Salinity**	**Depth (mean)**	**Depth (min)**	**Depth (max)**	**Distance from coastline**
ET	Fernando de Noronha	3°50'47.40"S 32°26'33.49"W	27.63	27.22	28.42	45.51	0.1	4.594	8.221	0.865	0.1182	36.132	6.5	6	7	360
ET	Atol das Rocas	3°52'22.11"S 33°48'32.66"W	27.44	27	28.16	46.24	0.11	4.594	8.200	0.861	0.1208	36.128	2.7	1.5	4	510
ET	Natal	05°25'S 35°14'W	27.76	27.42	28.35	45.37	1.22	4.617	8.173	0.941	0.1291	36.373	9.5	1	18	7
TR	Tamandaré	8°43'30.756"S 35°5'19.32"W	27.97	27.59	28.4	45.25	1.14	NA	NA	NA	NA	NA	2	1	3	0.1
TR	Maragogi	9°1'57.684"S 35°11'33.72"W	27.76	27.42	28.11	45.28	0.66	4.620	8.129	1.021	0.1284	36.852	3	2	4	1.8
TR	Salvador	12°46'14.42"S 38°37'9.07"W	27.85	27.33	28.26	41.86	3.1	4.742	8.071	0.782	0.1469	37.078	6	5	7	0
TR	Guarapari	20°42'0.58"S 40°24'24.59"W	23.83	23.29	24.58	39.42	1.21	4.919	8.045	1.288	0.2164	36.332	13	10	16	7
WT	Arraial do Cabo	22°57'54.96"S 41°59'37.31"W	23.5	22.77	24.16	38.42	0.81	5.133	8.135	1.584	0.2504	35.694	4	3	5	0
WT	Ilhabela	23°49'43.31"S 45°23'35.35"W	24.2	23.21	24.89	34.48	1.56	5.124	8.057	1.658	0.2524	35.577	7.5	4	11	1.6
WT	Florianópolis	27°12'11.11"S 48°22'59.45"W	22.5	21.69	23.19	34.71	1.33	5.308	8.065	1.194	0.2863	35.155	7	5	9	4

We recorded 102 macroalgae taxa across all sites, 90% belonging to the phylum Rhodophyta, 6% from Chlorophyta and 4% from Phaeophyceae. Only nine taxa, all belonging to calcareous articulated (CA) algae, accounted for 83% of the total biomass from all sampled sites. The maximum taxonomic richness of turf-forming algae and the lowest percentage of biomass contribution occurred among filamentous algae, which included 41 species from the three major phyla, representing 1.5% of total biomass. Corticated terete and foliose algae represented 12% and 3% of total biomass. Among all identified species, 48 were restricted to one site, 35 were restricted to one region whereas only one (*Gelidium crinale*) was found in all assemblages.

In the extreme tropical region, 61 taxa were recorded, 62% being from Rhodophyta, 25% from Phaeophyceae and 13% from Chlorophyta. Among all the species found in this region, 15 taxa were restricted to these sites, being absent in tropical and warm temperate ones. CA showed the highest biomass, with 7 taxa comprising 50% of total biomass and corticated terete comprised the functional group with the highest species number (37 taxa).We found 45 taxa of macroalgae in the tropical region, 69% being from Rhodophyta, 18% from Phaeophyceae and 13% from Chlorophyta. From this total, 6 taxa were exclusively found in the tropical sites. As was found for the extreme tropical region, CA algae were also the functional group with the highest biomass, representing 91% of total weight and comprising only 6 taxa, and corticated terete also comprised the functional group with the highest species number (24 taxa). In the warm temperate region we found 63 taxa of macroalgae, 62% being from Rhodophyta, 21% from Chlorophyta and 17% from Phaeophyceae. From this total, 14 taxa were exclusively found in warm temperate sites. As was found in both regions above, CA algae were also the functional group with the highest biomass, representing 87% of total weight, comprising 3 taxa, and corticated terete comprise the functional group with the highest species number (31 taxa) (Table S1).

GLM analysis showed that mean depth and mean SST were negatively related to richness, while PAR and Nitrate were positively related. The model with these four explanatory variables showed a pseudo-$R^2 = 0.373$. GLM analysis showed no differences among regions, when richness was considered (Table 2). The bivariate relationships between richness and selected environmental variables are presented in Figure 1. The total biomass was negatively related to mean depth, and positively related to PAR, coastal distance and nitrate. The model with these four explanatory variables presented a pseudo-$R^2 = 0.448$. GLM analysis showed that the tropical region had the highest total biomass, while the extreme tropical region had the lowest (Table 3). The bivariate relationships between the total biomass and the selected environmental variables are presented in Figure 2.

Table 2: Generalized Linear Model Analysis (GLM) considering the measured factors that influenced species richness significantly ($p<0.05$)

	Estimate	**Std. Error**	**Z**	**P**
Intercept	2.753	0.929	2.962	0.003
Mean depth	-0.020	0.009	-2.224	0.026
Mean SST	-0.132	0.044	-2.978	0.003

PAR	0.055	0.022	2.514	0.012
Nitrate	0.524	0.202	2.598	0.009

Table 3: Generalized Linear Model Analysis (GLM) of biomass considering the measured factors that influenced them significantly ($p<0.05$)

	Estimate	Std. Error	t	P
Intercept (Extreme tropical)	-11.771	3.424	-3.437	0.001
Mean depth	-0.073	0.031	-2.378	0.019
PAR	0.223	0.076	2.945	0.004
Distance to coast	0.002	0.001	2.173	0.032
Nitrate	2.037	0.833	2.446	0.016
Tropical	2.207	0.418	5.280	0.000
Warm-Temperate	1.955	0.951	2.055	0.042

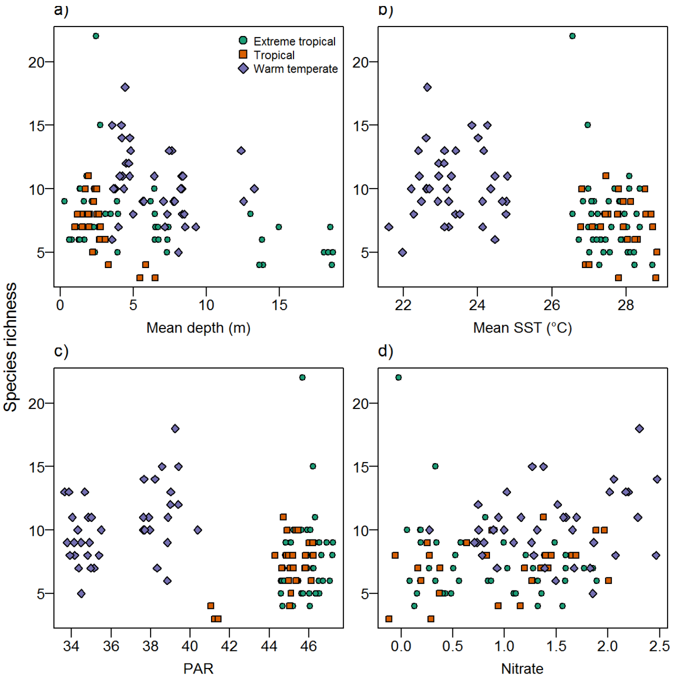


Figure 1: Bivariate relation between environmental variables and species richness

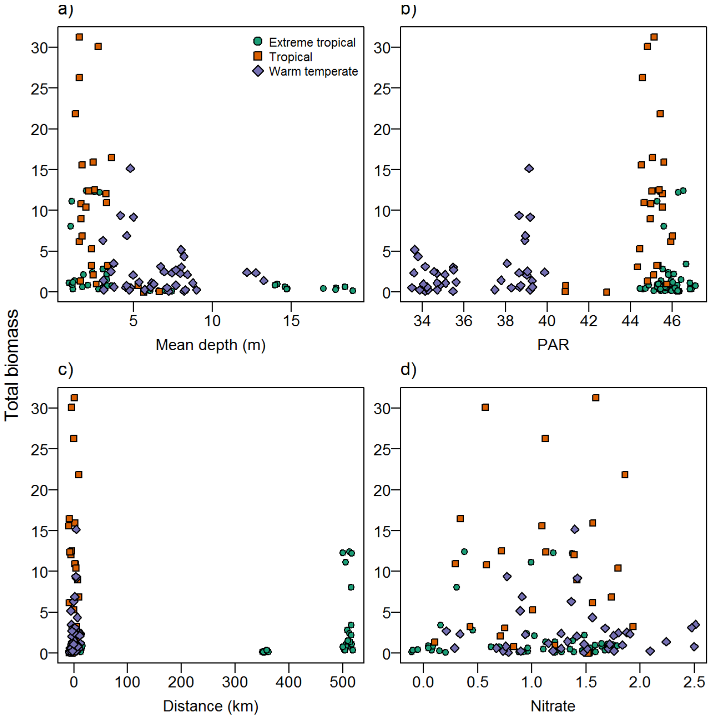


Figure 2: Bivariate relation between environmental variables and total biomass

The PCOA analysis indicated some differences in species composition and biomass between tropical and other regions, and few differences between extreme-tropical and warm-temperate regions (Figure 3). PCOA analysis also indicated a positive relation between mean depth and 3 turf species: *Laurencia* sp., *Canistrocarpus crispatus* and *Dictyopteris* sp. 1, and a negatively relation with *Gelidium floridanum* and *Gelidium pusillum*. Mean SST was positively related to *Champia minuscula*, *Hypnea spinella*, *Jania adhaerens*, *Lobophora* sp. and *Padina* sp. and negatively related to *Asparagopsis taxiformis*, *Chondracanthus acicularis*, *Gelidiella acerosa*, *Hypnea musciformis*, *Jania prolifera*, *Cladophora* sp., *Dictyopteris* sp. 1 and *Sargassum* sp. PAR was positively related to *Asparagopsis taxiformis*, *Centroceras* sp., *Hypnea musciformis*, *Jania prolifera*, *Polysiphonia* sp., *Cladophora* sp., *Cladophora vagabunda*, *Padina* sp., and *Sargassum* sp. and negatively related to *Amphiroa* sp., *Centroceras clavulatum*, *Chondracanthus acicularis*, *Gelidium crinale*, *Gelidium floridanum*, *Gelidium pusillum*, *Hypnea spinella*, *Caulerpella ambigua*, *Canistrocarpus crispatus* and *Sphacelaria* sp. The distance from coastline was positively related to 5 species: *Gelidium floridanum*, *Laurencia* sp., *Canistrocarpus cervicornis,Canistrocarpus crispatus* and *Dictyopteris delicatula* and negatively related to *Chondria polyrhiza* , *Digenea simplex*, *Jania adhaerens*, *Cladophora* sp. and *Valonia* sp. Nitrate was positively related to*Canistrocarpus cervicornis* and *Sargassum* sp. and negatively related to 7 species: *Ceramium* sp., *Champia minuscula*, *Digenea simplex*, *Hypnea spinella*, *Jania adhaerens*, *Plocamium brasiliense* and *Caulerpella ambigua*.

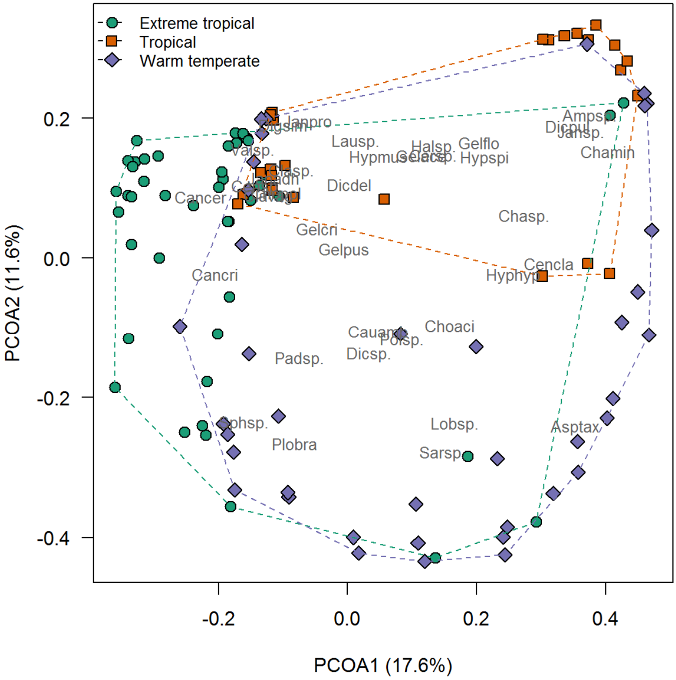
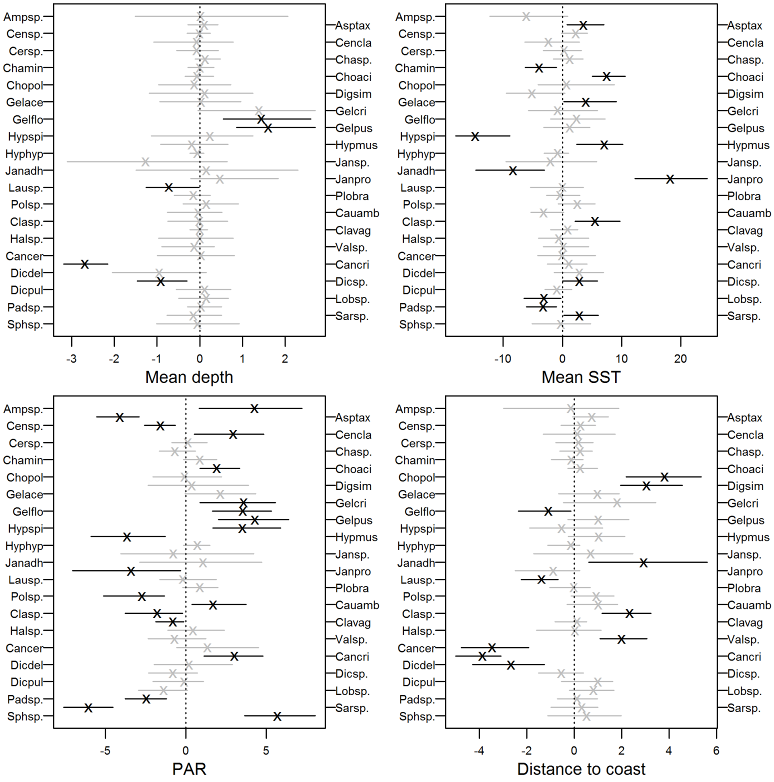


Figure 3: Model-based ordination plot for species biomass and composition of turf species. The plot indicates the main differences in the species matrix that can be attributed to random site effects. The three regions are indicated to help interpretation of the patterns and species codes in bold indicate species with significant differences among regions. Only species with occurrence in at least seven sites were used in the analysis. The names of the species were abbreviated to three letters of the genus and three letters of the specific epithet

The tropical region showed higher biomass than the extreme tropical region for 4 species: *Canistrocarpus cervicornis*, *Canistrocarpus crispatus*, *Dictyopteris delicatula* and *Dictyopteris* sp. 1; and lowest biomass than extreme tropical for 6 species: *Amphiroa* sp., *Gelidiella acerosa*, *Gelidium crinale*, *Hypnea spinella*, *Jania prolifera* and *Halimeda* sp. The warm temperate region showed higher biomass than the extreme tropical region for 4 species: *Hypnea spinella*, *Jania adhaerens*, *Lobophora* sp. and *Padina* sp.; and lower biomass than the extreme tropical region for 7 species: *Chondracanthus acicularis*, *Gelidiella acerosa*, *Gelidium floridanum*, *Gelidium pusillum*, *Jania prolifera*, *Cladophora* sp., and *Sphacelaria* sp. The extreme tropical region presented higher biomass than the tropical region for 11 species: *Amphiroa* sp., *Gelidiella acerosa*, *Gelidium crinale*, *Gelidium floridanum*, *Gelidium pusillum*, *Hypnea spinella*, *Hypnea musciformis*, *Jania* sp., *Jania adhaerens*, *Jania prolifera*, and *Halimeda* sp.; and lowerbiomass for 4 species: *Canistrocarpus cervicornis*, *Canistrocarpus crispatus*, *Dictyopteris delicatula*, and *Dictyopteris* sp.1 (Figure 4).


Ampsp.
Censp.
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Hypspi
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Janadh
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Halsp.
Cancer
Dicdel
Dicpul
Padsp.
Sphsp.
Asptax
Cencla
Chasp.
Choaci
Digsim
Gelcri
Gelpus
Hypmus
Jansp.
Janpro
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-3
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Distance to coast

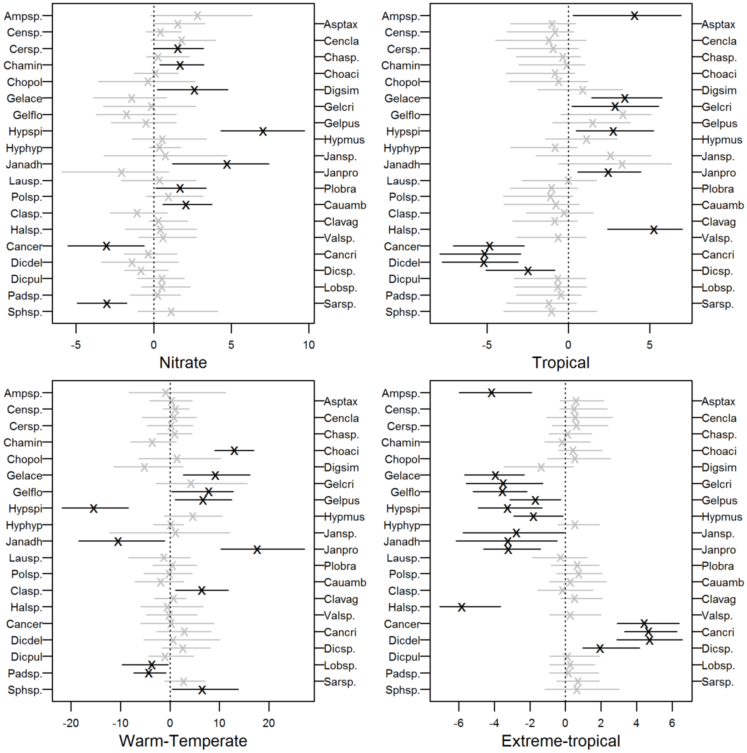

Figure 4: Relationship between each species biomass and environmental variables. Each panel shows the relationship of all species with an environmental variable. For each species, the highest posterior density (HPD) interval is indicated and intervals not including zero are considered significant. In addition, significant correlation of species and environmental variables are indicated in black and not significant in gray. Significant HPD intervals indicate also whether the association is positive (HPD interval to the right) or negative (HPD interval to the left)

4. DISCUSSION

This study provides the first thorough description of the composition and biomass variation of turf algal assemblages on many reef sites across different large marine ecosystems structured by all main macroecological drivers. The general pattern observed to each latitudinal range provides evidence that the main drivers determining patterns of the macroalgal community (Horta et al. 2001) also act at small turf algae scale, influencing the distribution and occurrence of these primary producers. On the other hand, independent of physical and chemical environmental factors, a general physiognomy emerged in all regions. This pattern is produced by the frequent dominance of *Jania* sp. and *Amphiroa* sp., articulated coralline algae which showed the highest biomass in most of three macro regions.

Higher values of PAR and SST near the tropics corroborate the dominance of CA algae as they present ecophysiological adaptations that minimize photo damage and maximize photosynthetic production (Burdett et al. 2014). We found positive correlation between biomass and SST (variation) and between biomass and PAR. On the other hand, the filamentous constituents of turf assemblages receive protection against UV and PAR irradiance, providing a pH buffer in their microclimate and stimulating calcification and growth of CA algae (Short et al. 2015). These complex, but precise interactions, considering the availability of irradiance, CO2 and nutrients, could be responsible for the internal regulation of the observed community structure. With the increase of nutrient concentration, influenced by the continental runoff, CA algae are negatively affected, favoring algae with or without chemical defenses – which would depend on the herbivorous pressure in a particular location. While high nutrient concentration and low SST negatively affect CA algae richness, these factors coupled with low irradiance produce appropriated conditions for the development of filamentous and, in many times, opportunistic species (Martins et al. 2012).

These calcareous articulated algae, while containing comparatively high levels of calcium carbonate, tolerate high levels of herbivory by being ephemeral and having high turnover rates (Steneck 1985, Hackney et al. 1989). On shallow reefs, for example, fishes can take over 100,000 bites/m^2/day, consuming almost all benthic algal production (Hatcher 1982, Carpenter 1986, Hay 1991, Bruggemann 1994, Ferreira et al. 1998). Among the sites that were not dominated by CA algae, two of them, both located in the extreme tropical region, were dominated by *Canistrocarpus* spp. Although they present chemical deterrent properties (Hay & Steinberg 1992, Bianco et al. 2010), these species are rich in lipids (McDermid et al. 2007) and are a common item in the diet of many species of herbivorous/detritivorous surgeon and parrotfishes (Ferreira & Gonçalves 2006, Longo et al. 2015, Clements et al. 2016).

CA algae was also not dominant in BA site, where *Gelidium* sp. presented the highest biomass. This genus does not have any kind of defense against herbivores, but it is a common component within turfs in many reef sites of Brazilian coasts (Ferreira et al. 1998, Mendes et al 2009, Longo et al. 2015).

Its dominance in a tropical region may indicate a low abundance of herbivores or a decrease in the water quality. Both situations could be explained by intense anthropogenic disturbances, including overfishing and discharge of domestic and industrial sewage (Costa Jr et al. 2000, Amado-Filho et al. 2001, Littler et al. 2006, Marins et al. 2008). This input of pollutants in coastal environments can lead to an increase in DIN concentrations or to an acidification of seawater (Noriega & Araujo 2014), which would preclude the occurrence or decrease the growth and calcification of coralline algae in these locations (Björk et al. 1995, Hall-Spencer et al. 2008, Semesi et al. 2009).

Our findings suggest that physical environmental factors, especially SST and PAR, strongly influence large-scale distribution patterns of turf-forming algae species along a latitudinal gradient off southwestern Atlantic. However, herbivory seems to drive dominant species abundance in a regional scale, as it apparently promotes selective consumption of some algae, providing niche availability to coralline red algae. Experimental studies are required to better understand the causal relations in algal turf assemblage structure, as the covariance of other factors compromise the robustness of most plausible ecological answers.

Although algal turf is seldom taxonomically assessed and its specific richness is usually underestimated, some authors have reported that the composition of turfs in some Brazilian coral reef systems is mainly dominated by the geniculated corallines *Jania*, *Amphiroa* and *Haliptilon* (sensu *Jania*), corroborating the results found in this work. Red and brown algae, such as *Anthithamnion*, *Ceramium*, *Digenea*, *Griffithsia*, *Gelidium* and *Sphacelaria* are also common components of algal turfs. Some green algae can also be present, mainly *Enteromorpha*, *Cladophora* and *Bryopsis*, as reported by previous authors (Figueiredo 1997, Villaça & Pitombo 1997, Costa et al. 2002). The composition of turfs in Brazilian coral reefs is similar to reefs of the Caribbean (Adey 1998, Steneck 1988) and Great Barrier (McCook et al. 2001). The presence of young macroalgal species normally found as canopy-forming algae reinforce the role of this assemblage working as facilitator of settlement (Coull & Wells 1983).

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COMPLIANCE WITH ETHICAL STANDARDS

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CAPÍTULO 3

Spatial variability of chemical compounds in turf assemblages from Southwestern Atlantic

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MARTINS, C.D.L. et al. Spatial variability of chemical compounds in turf assemblages from Southwestern Atlantic.

SPATIAL VARIABILITY OF CHEMICAL COMPOUNDS IN TURF ASSEMBLAGES FROM SOUTHWESTERN ATLANTIC

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ABSTRACT

Macroecological factors and biotic interactions may influence the structuring of marine communities at different scales. Temperature and PAR are predicted by multiple hypotheses to be strongly correlated with species richness and abundance of macroalgae forming a latitudinal gradient. These patterns of diversity may also be observed in the metabolic expression of organisms. Therefore, the aim of this study was to investigate if sugar, reserve carbohydrate (RC) and phenolic compounds concentrations from turf assemblages differed along Southwestern Atlantic and if this variation was related to local and broad-scale abiotic environmental gradients. Our results illustrate remarkable differences in chemical compounds from turf algae assemblages along Southwestern Atlantic. The highest RC concentration was found in warm temperate region, while phenolic compounds were higher in extreme tropical region. The major ecological factors driving their content in turf assemblages were SST and PAR. This leads us to reinforce the hypothesis that macroecological factors may not only determine the structuring of algae communities, but also the production of their primary and secondary metabolites, as they represent a direct result of physiological adaptations to specific environmental conditions.

Key Words: Turf, Macroecology, Metabolites, Latitudinal pattern

1. INTRODUCTION

Spatial scales have become increasingly important source of questions in ecology because pattern drivers and identification of their causal mechanisms are still misunderstood (Levin 1992, Peterson & Parker 1998, Gardner et al. 2001) despite its importance as integrative basis for modern ecology (Azovsky et al. 2000). In many ecosystems, the smallest scales are drived by stochastic events or processes, producing fractal patchiness, while at larger scales these processes become more generalizable as macroecological or biogeographical patterns (Levin 1992, Coleman 2002, Fraschetti et al. 2005). Summarizing these macroecological patterns in marine ecosystems, we can state that environmental factors influence the structuring of a community more strongly at high latitudes (Pianka 1966, Keith et al. 2014). Among them, sea surface temperature (SST) and photosynthetic active radiation (PAR) are predicted by multiple hypotheses (ambient energy, productivity; Willig et al. 2003) to be positively correlated with diversity, and they have been found to be strong predictors of species richness for higher marine taxa that follow the latitudinal diversity gradient (Tittensor et al. 2010). However, macroalgal diversity does not peak in the tropics (Bolton 1994, Kerswell 2006, Santelices et al. 2009). Instead, the location of distributional limits of multiple macroalgal species suggests that extreme temperatures may limit diversity (van den Hoek 1982, Luning 1990, Steneck et al. 2002, Bartsch et al. 2012). On the other hand, biotic interactions are hypothesized to become relatively more important than environmental conditions as drivers of large-scale diversity gradients at low latitudes (Pianka 1966, Keith et al. 2014). Grazing and competition (Steneck & Dethier 1994) are two of the most dominant biological processes that drive succession and thus heterogeneity in community structure. For macroalgae, competition with corals and increased predation pressure are hypothesized to inhibit diversity within the tropics (Gaines & Lubchenco 1982, Bolton 1994). In other words, and connecting these general spatial patterns with some ecological concepts, the structuring of these communities in temperate regions can be explained by the Court Jester model, while in tropical environments can be explained by the Red Queen model (Benton 2009). These patterns of diversity described above can be observed in different plots of the community or even in the metabolic expression of organisms, but very little is discussed about the metabolism of these assemblages.

Considering the hypothesis that the production of primary and secondary metabolites is a result of physiological and metabolic feedbacks of populations and communities with their environments (Martins et al. 2014), the spatial variation of these metabolites may represent an important descriptor to understand the mechanisms responsible for these macroecological patterns. In general, the levels of primary metabolites, especially starch-like polymers or reserve carbohydrates (RC), reflect a balance between chemical energy production, with photosynthesis, and consumption, with cellular respiration. This energy is transformed in thallus growth or biosynthesis of primary and secondary metabolites.

Although these secondary metabolites have no direct function on growth and development, they play a key role in their interaction with the environment, being usually responsible for the synthesis of chemical defenses (Taiz & Zeiger 1991). The biological effects of these metabolites represent key evolutionary and macroecological role once allelopathic and deterrent compounds shaped herbivorous behaviours and traits, once they reduce their digestibility or have the capacity to convert tissues as toxic or unpalatable (Amsler & Fairhead 2006). Then it is possible to assume that these secondary metabolites are also a consequence of evolutionary pressure of biological interactions as herbivory, as proposed by Hay (1984). However, polyphenolic compounds are secondary metabolites whose functions may also include protecting from damage by ultraviolet radiation, besides deterring feeding by herbivores (Van Alstyne et al. 1999, Collen et al. 2007).

Therefore, following the latitudinal gradient of temperature and irradiance, it would be expected to find an increase in the metabolic rates, in response to higher values of these environmental factors at lower latitudes, enhancing photosynthetic potential production and respiration rates. Thus we can expect an optimum production of primary metabolites and eventually a higher concentration of reserve carbohydrates in areas where temperature, irradiance and nutrients are suitable available and the use of resource by macroalgae is optimum. Therefore we could expect a more abundant production of secondary metabolites in areas with higher intensity of biological interactions and/or where the oxidative stress caused by ultraviolet radiation is higher.

Among marine primary producers, turf-forming macroalgae are among the most productive members (Hay 1981, Carpenter 1985, Klumpp & Mckinnon 1989, Wilson et al. 2003). In particular, dense turf communities have some of the highest production rates ever measured on a reef, equal to or greater than coral and crustose coralline algae (Wanders 1976). Turf algae are more abundant than both coral and other macroalgae on many coral reefs (Wismer et al. 2009), and are likely to become more abundant in the future, because they thrive under conditions that threaten coral health, such as overfishing of herbivores, nutrient pollution (Smith et al. 2010), ocean acidification (Falkenberg et al. 2013), and sedimentation (Birrell et al. 2005). Turf algae can be particularly difficult to study due to the inconsistency in how researchers categorize them, their diversity in different ecosystems, and the tendency for scientists to group them together with other benthic organisms. Despite this, the reduced size of the constituents of this assemblage contribute to their utilization in the community metabolic description once a sample with a relatively small area presents all main populations present in a certain site. Two common synonyms for turf algae are the ‘epilithic algal community (EAC) (Hatcher & Larkum 1983, McCook 1999) and ‘epilithic algal matrix (EAM) (Wilson et al. 2003), though the latter specifically includes invertebrates, detritus, and microbes in addition to algae. In this paper, the term “turf algae” specifically refers to only the algal component of the community.

In this study, we posed the following questions: (1) Do differences in sugar, reserve carbohydrates and phenolic compounds concentrations occur among regions along Southwestern Atlantic and, if so, does this variation form a latitudinal cline? and (2) Do these metabolites concentrations related to local and broad-scale abiotic and biotic environmental gradients? To address these questions we measured soluble sugars, reserve carbohydrates and phenolic compounds concentrations in turf assemblages collected from nine sites along Southwestern Atlantic.

2. METHODS AND MATERIALS

2.1 Study region and data collection

Algal turfs were sampled in nine reef sites along 4000 Km of coastline in the southwestern Atlantic (Figure 1), from January 2012 to August 2013, through total scraping of 100 haphazardly placed quadrats (0.01 m^2 each). These sites were aggregated into 3 regions, based on the latitudinal proximity among them: three sites represented the extreme tropical region (ET), including two oceanic islands, four sites represented the tropical region (TR), while three represented the warm temperate region (WT). For sample collections, turf was defined as distinct mats of low-growing algae <5 cm canopy height. The coordinates from each sampling site were taken thereafter from GoogleEarth® (version 7.1.2.2041). Environmental factors were also evaluated from each site: (1) annual mean, minimum and maximum values of sea surface temperature (SST), (2) photosynthetically active radiation (PAR), (3) Chlorophyll *a*, (4) oxygen, (5) pH, (6) nitrate, (7) phosphate and (8) salinity were extracted from MODIS Aqua Ocean Level-3 standard mapped archive products (Feldman & McClain 2012), produced and distributed by the NASA Goddard Space Flight Center's Ocean Data Processing System (ODPS) (data from 2003 to 2013); (9) means, minimum and maximum depths of sampling were taken *in situ*; and (10) distance of each site from the coastline was calculated using satellite images taken from GoogleEarth®. Turf biomass and richness of each quadrat and their respective means per site were extracted from Martins et al. (*no prelo*). In laboratory, samples were washed with seawater to remove sand and epifauna and with ammonium formiate to remove salts from macroalgae thalli.

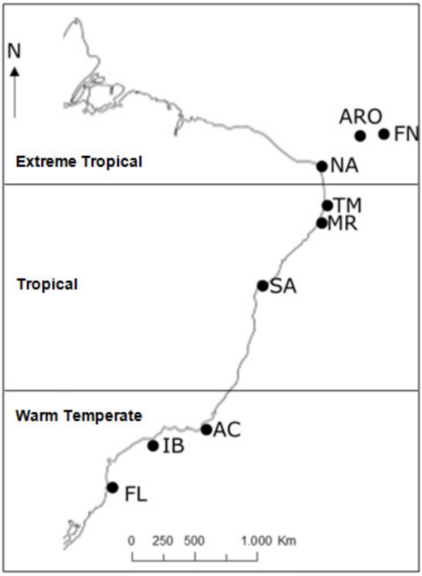

Figure 1: Sites where samples were collected ("FN" for Fernando de Noronha, "ARO" for Atol das Rocas, "NA" for Natal, "TM" for Tamandaré, "MR" for Maragogi, "SA" for Salvador, "AC" for Arraial do Cabo, "IB" for Ilhabela

and "FL" for Florianópolis) and their corresponding region ("ET" for extreme tropical, "TR" for tropical and "WT" for warm temperate)

2.2 Turf chemical analyses

In laboratory, seaweeds were washed with seawater to remove sand and epifauna from their thalli and with ammonium formiate to remove salts. Each square sample were dried at 38°C (± 2°C) for 24 hours, pulverized together in liquid nitrogen and stored in a freezer for subsequent nutritional analyses.

2.2.1 Total soluble sugars content

The extraction of total soluble sugars was performed according to Shannon (1968). An aliquot of 0.05 g of dry weight of each turf sample (n=6) was extracted with 2 ml of methanol, chloroform and distilled water solution (12:5:3) and centrifuged at 3000 rpm for 5 minutes. The supernatant was collected and the precipitate was extracted again as above specifications. To four parts of supernatant were added one part of chloroform and one and a half part of distilled water. This extract was centrifuged at 3000 rpm for 5 minutes and the upper aqueous solution was collected and analyzed according to Umbreit et al. (1957), using the reagent anthrone 0.2% (w/v). Before being read in a spectrophotometer at 620 nm, the samples were shaken in a vortex and heated at 100°C for 3 minutes. Total soluble sugar concentration was calculated using D-glucose (10 to 100 $\mu g.mL^{-1}$, $r^2 = 0.996$, $y = 0.014x$) as standard and expressed as mg of total soluble sugars per g of dry matter.

2.2.2 Total reserve carbohydrates content

The reserve carbohydrate (RC) extraction was performed according to McCready et al. (1950). The residues of the samples used for the determination of total soluble sugars were extracted with perchloric acid ($HClO_4$) 30% (v/v) and centrifuged at 3000 rpm for 5 minutes. The supernatant was collected and the precipitate was extracted again as above specifications. The extract was centrifuged and the supernatants of both extractions were pooled and analyzed according to Umbreit et al. (1957), using the reagent anthrone 0.2% (w/v). The samples were shaken in a vortex, heated at 100°C for 3 minutes and read at 620 nm in a spectrophotometer. The RC concentration was estimated using D-glucose (10 to 100 $\mu g.mL^{-1}$, $r^2 = 0.997$, $y = 0.007x$) as standard and expressed in mg of RC per g of dry matte.

2.2.3 Phenolic Compounds

The analysis of phenolic compounds was made using the spectrophotometric method of Folin-Ciocalteau based on Arnaldos et al. (2001) with modifications based on Schiavon (2012). Phenolic compounds were extracted from 0.1 g of dry weight turf samples (n=3), using 5 mL of 80% aqueous methanol. The extracts were centrifuged for 10 min at 4000 rpm. Aliquots of 200 μL of supernatant crude extracts, 150 μL of Folin reagent and 1.650 mL of sodium carbonate 2% w/v, were mixed and incubated at room temperature for 1 hour. Absorbance of the reaction mixture was measured at 750 nm, using a spectrophotometer (Gold Spectrum lab 53 UV-Vis spectrophotometer, BEL photonics, Brazil). The quantification of the total phenolic compounds was done from the standard curve of gallic acid (50 to 800 μg.mL^{-1}, $r^2 = 0.99$, $y = 1.344x$) and expressed in mg of phenolic per g of dry matter.

2.3 Data analysis

Total sugars, RC and phenolic compounds concentrations were log transformed to pass the assumptions of normality and homogeneity of variance. To test for differences in metabolites concentrations among regions we used a two-way nested analysis of variance (ANOVA) with site nested within region followed by Tukey's HSD post hoc tests.

Then, the relationships between sugar, RC and phenolics with potential explanatory variables were explored using bivariate plots. In all cases, turf biomass and richness and the abiotic factors maximum SST, nitrate, PAR, maximum depth, distance from coastaline and classification by three regions were considered as potential predictors. All other abiotic variables were removed after a preliminary round of analyses as they were redundant with the information contained in this subset of variables. Next, sugar, RC and phenolics were modeled with generalized linear models (GLM). Sugar, RC and phenolics were best modeled using Gamma distribution with logarithmic link function (against normal distribution) and the set of candidate explanatory variables model simplification was carried out using Akaike Information Criterion (AIC). To test for effects of variables on sugar, RC and phenolics we used a model-based approach. This approach is known as model-based ordination and resulted in an ordination biplot scaled for both compounds and sites (Hui et al. 2015). We then assessed the importance of biomass, richness, maximum SST, nitrate, PAR, maximum depth, distance from coastaline and classification by three regions as potential drivers of changes on sugar, RC and phenolics between sites with a correlated response GLM (Hui et al. 2015, Warton et al. 2015). Pure latent variable model and correlated response GLM were calculated using R program 3.4.1 (R Core Team 2017).

3. RESULTS

The extreme tropical province was characterized by higher water temperature (both minimum and maximum values) and irradiance values, when compared to tropical and warm temperate regions. The maximum SST ranged from 23.2ºC (in a warm temperate site) to 28.4 ºC (in both extreme tropical and tropical sites). PAR values ranged from 34.4 $uE.cm^{-2}.s$ (in a warm temperate site) to 46.2 $uE.cm^{-2}.s$ (in a extreme tropical site). The sampling depths ranged from 1 to 18 meters among extreme tropical sites, from 1 to 16 meters among tropical and from 3 to 11 among warm temperate ones. The distances of sampling sites from the nearest point on the coastline were 7, 360 and 510 kilometers in the extreme tropical region, the last two corresponding to oceanic islands. Among tropical sites this distance ranged from 0 to 7 kilometers and among warm temperate sites it ranged from 0 to 4 kilometers. According to Martins et al (*no prelo*), richness ranged from 3.33 to 11.73 (mean values in 0.01 m^2), while biomass ranged from 0.19 to 14.76 (mean values in 0.01 m^2).

Total soluble sugar concentration did not show any difference among the three regions (Table 1). Average RC (Table 2) and phenolic compounds concentration (Table 3) of turf assemblages were significantly different among regions. The highest RC concentration was found in warm temperate region, followed by tropical region, while extreme tropical showed the lower average values. On the other hand, phenolic compounds concentration was higher in extreme tropical region, followed by warm temperate, while the lowest values were found in tropical region.

Table 1: Results of two-way nested analysis of variance (ANOVA) comparing total soluble sugars among sampled regions

	DF	SumSq	MeanSq	F Value	Pr (>F)
Region	2	0.19	0.93	0.22	0.806
Region (Site)	6	33.81	5.63	13.03	<0.001
Residuals	96	41.52	0.43		

Table 2: Results of two-way nested analysis of variance (ANOVA) comparing reserve carboydrate concentration among sampled regions

	DF	SumSq	MeanSq	F Value	Pr (>F)
Region	2	27.53	13.76	43.76	<0.001
Region (Site)	6	83.06	13.84	44.01	<0.001
Residuals	96	30.20	0.31		

Table 3: Results of two-way nested analysis of variance (ANOVA) comparing phenolic compounds concentration among sampled regions

	DF	SumSq	MeanSq	F Value	Pr (>F)
Region	2	43.65	21.82	67.32	<0.001
Region (Site)	6	44.07	7.35	22.66	<0.001
Residuals	98	31.77	0.32		

GLM analysis showed that total soluble sugars content was also positively related to PAR and negatively related to SST (maximum values), total biomass and richness of turf algae (Table 4). The model with these four explanatory variables presented a pseudo-R² = 0.418. The bivariate relationships between sugars content and selected variables are presented in Figure 2. In opposite, RC content was positively related to SST (maximum values) and depth (maximum values) and was negatively related to total biomass of turf algae (Table 5). The model with these three explanatory variables presented a pseudo-R² = 0.496. The bivariate relationships between RC content and selected variables are presented in Figure 3. Phenolic compounds was negatively related to depth (maximum values) and distance from coastline (Table 6). The model with these two explanatory variables presented a pseudo-R² = 0.793. The bivariate relationships between phenolic compounds and selected variables are presented in Figure 4.

Table 4: Generalized Linear Model Analysis (GLM) considering the measured factors that influenced total soluble sugars content significantly ($p<0.05$)

	Estimate	Std. Error	t value	Pr(>|t|)
Intercept (Extreme	5.291	1.490	3.551	<0.001

tropical)				
SST max	-0.820	0.118	-6.921	<0.001
PAR	0.375	0.053	7.057	<0.001
Biomass	-0.031	0.013	-2.429	0.017
Richness	-0.075	0.027	-2.810	0.006

Table 5: Generalized Linear Model Analysis (GLM) considering the measured factors that influenced total RC content significantly ($p<0.05$)

	Estimate	Std. Error	t value	Pr(>|t|)
Intercept (Extreme tropical)	-25.435	5.998	-4.240	<0.001
SST max	1.085	0.190	5.697	<0.001
Depht max	0.076	0.021	3.558	<0.001
Biomass	-0.029	0.014	-2.053	0.043
Class2Tropical	0.787	0.249	3.160	0.002
Class2Warm temperate	4.144	1.000	4.143	<0.001

Table 6: Generalized Linear Model Analysis (GLM) considering the measured factors that influenced phenolic compounds significantly ($p<0.05$)

	Estimate	Std. Error	t value	Pr(>|t|)
Intercept (Extreme tropical)	0.1879600	0.2464007	0.763	0.4473
Depht max	-0.041	0.017	-2.368	0.020
Distance	-0.005	0.001	-11.058	<0.001
Class2 Tropical	-3.402	0.232	-14.678	<0.001
Class2 Warm temperate	-2.464	0.189	-13.018	<0.001

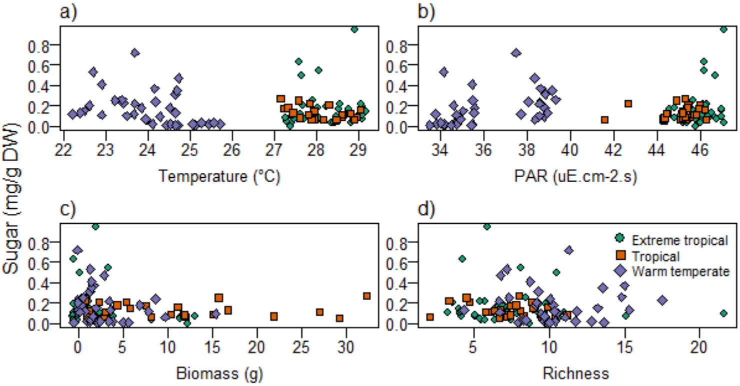

Figure 2: Bivariate relation between maximum sea surface temperature (ºC), PAR (uE.cm^{-2}.s), turf biomass (g) and turf richness with total soluble sugars content (mg/g of dry weight)

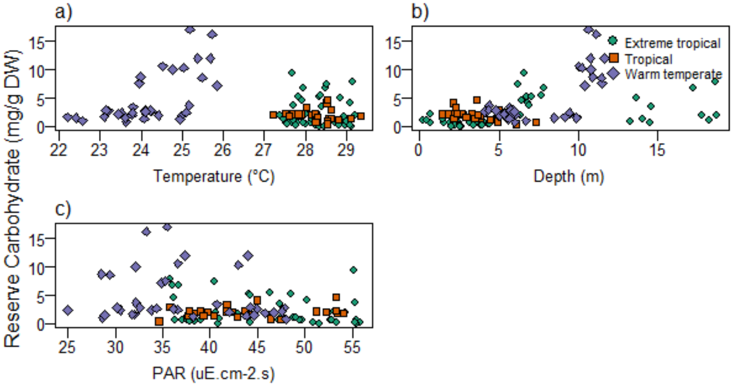

Figure 3: Bivariate relation between maximum sea surface temperature (ºC), maximum depth (m) and PAR (uE.cm^{-2}.s) with total reserve carbohydrate content (mg/g of dry weight)

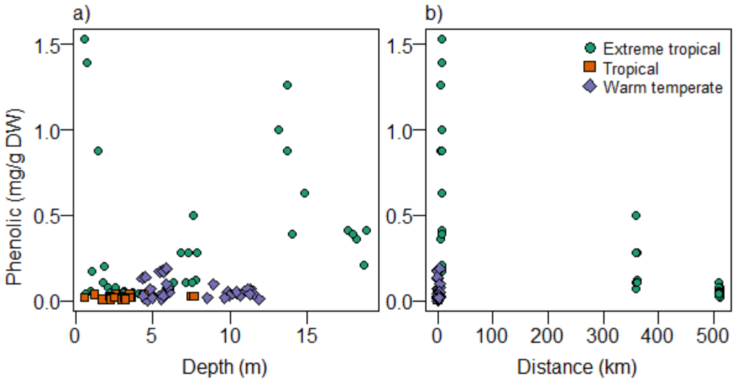

Figure 4: Bivariate relation between maximum depth (m) and distance from the coastline (Km) with phenolic compounds concentration (mg/g of dry weight)

4. DISCUSSION

Our results illustrate remarkable differences in chemical compounds from turf algae assemblages along Southwestern Atlantic. The major ecological factors driving the assemblage metabolism were SST and PAR. Both of them were also determinants for large-scale patterns of turf-forming algae assemblages structure from the same region, as already reported by Martins et al. (*no prelo*). This leads us to reinforce the hypothesis that the same macroecological factors that determine the structuring of a benthic community may also determine their synthesis of primary and secondary metabolites, as they represent a direct result of physiological adaptations to specific environmental conditions.

Most of published works relating the variation in RC and sugar concentrations in response to environmental and biological variables come from plants, while few studies were published considering results from algae. In general, non-structural carbohydrates (NSCs), mainly composed of soluble sugars and RC, starch like polymers (SLP), are used in metabolic processes of photosynthesis, respiration and production (Koch 1996, Van den Ende et al. 1999). In plants, the content of NSCs and their composition (ratio of glucose:RC) reflect the balance between carbon sources and sinks (Chapin et al. 1990, Hoch et al. 2003, Würth et al. 2005) and indicate the adaptive strategies to changing environments (Koch 1996, Loewe et al. 2000). According to the growth limitation hypothesis, if tissue formation is limited with decreasing temperature, the content of NSCs should increase because of the decreased demand for structural carbon with no consideration of the limitation of nitrogen, phosphorus, and others (Körner 1998). The quantity of soluble sugars may increase under conditions of low temperature, because they are signal substances that enable adaptation to changing environment (Pan et al. 2002). The zonal distribution of PAR has also an apparent impact on NSCs content by regulating photosynthesis at a large geographical scale (Li et al. 2016). These agree with the observed higher accumulation of soluble sugars under lower temperature and higher incidence of PAR, as shown by this work. Accumulation of higher sugars concentration can significantly inhibits photosynthesis (Jang et al. 1997) and leads to stunted growth (Sonnewald et al. 1991). RC has also a negative relation to photosynthesis, once it is used as a relatively long-term energy storage in plants (Zhang et al. 2006, Li et al. 2008). These inverse relations between sugar and RC contents and photosynthesis were also observed by our work, if we consider the potential photosynthetic rates, growth and biomass as correlated measures. This also agrees with the observed higher accumulation of RC under higher depths, if we consider the potential photosynthetic rates decreasing as a consequence of depth increasing, regarding the attenuation of solar radiation (Nybakken 1993). Although the content of soluble sugars was positively correlated with PAR, a similar correlation was not observed for RC, possibly because these polymers were mainly stored as energy and therefore was affected less by PAR. An inverse relationship between RC content and growth can be found in some algae species, as already reported to *Gracilaria foliifera* and *Ulv*a spp. (Rosenberg & Ramus 1982). This was also observed by our work, if we consider biomass and growth as comparable descriptors.

Phenolic compounds concentration was higher in extreme tropical region and was negatively related to maximum depth of samples and their distances from the coastline. In other words, greater depths or distances from coastline were related to lower concentration of phenolic compounds in turf assemblages. According to Van Alstyne (1988), differences in phenolic levels may reflect (1) reasons not related to herbivore density, (2) local selection for better defended algae in locations where herbivory pressure is higher, or (3) production induced by herbivores. The reasons not related to herbivory may correspond to environmental factors that induce the production of these metabolites in photosynthetic organisms. Among these factors, solar radiation is well known for presenting a positive relation with phlorotannin production, as already reported for some algae (Yates & Peckol 1993). Thus, the most common explanation for phenolic production at the intraspecific level is the carbon/nutrient balance model (Bryant et al. 1983). According to this model the production of polyphenolics, and other C-based secondary metabolites, is governed by the relative supply of carbon (through photosynthesis) and essential nutrients. Consequently, polyphenolic production should increase under conditions of high UV irradiance (Hay 1996, Pavia et al. 1997, Pavia & Brock 2000, Mannino et al. 2014). An alternative, less often advocated explanation for the effect of solar radiation on polyphenolic production is that polyphenolics are produced as protection against photodestruction caused by ultraviolet (UV) light, acting as oxidant scavenging molecules (Pedersen 1984, Ragan & Glombitza 1986, Swanson & Druehl 2002, Jormalainen & Honkanen 2004). In these cases, phenolic production would be higher in areas with greater penetration of UV radiation in sea water, as the case of shallower areas of the coast or areas where water transparency is higher, as observed in this study. Indeed, UV-B incidence presents a stratification in the water column as a function of depth, dramatically decreasing in a few meters, depending on the transparency of water. According to Tedetti & Sempéré (2006), the 10% irradiance depth for UV-B (Z10% UV-B) calculated for coastal sea waters can range from 1.25 meters to 6.7 meters depth, while for open waters from Western Subtropical Atlantic Ocean can range from 13 to 15.5 meters depth. Besides that, phenolic compounds were higher in Natal and Fernando de Noronha, among all sampled sites. According to Martins et al. (*no prelo*), the dominant species at these sites were *Canistrocarpus* sp., *Dictyopteris* sp. and *Sphacelaria* sp., all from Phaeophyceae. In fact, phenolic compounds are most common and abundant in brown seaweeds, where they are composed of polymers of phloroglucinol, and often are referred to as phlorotannins (Ragan & Glombitza 1986). In addition to cellular functions, phenolic compounds act as allelopathic compounds and defend seaweeds against biological interactions, such as herbivory (Cronin & Hay 1996, Pavia & Toth 2000, Amsler & Fairhead 2006). Among their several kinds of adaptation to reduce their attractiveness and avoid or minimize the damage caused by herbivory, the production of phenolic compounds by seaweeds reduce thalli digestibility or nutritional qualities, or may become toxic or unpalatable (Hay et al. 1987, Paul et al. 2001, Pereira & Da Gama 2008). At low latitudes the biomass and species richness of herbivorous fishes are higher (Floeter et al. 2005, Vanderklift & Kendrick 2004, Poore et al. 2012) and in response, some macroalgal species are able to produce a greater concentration of defensive compounds than their sister species in temperate regions (Bolser & Hay 1996), as observed by this work. For example, some authors detected a higher concentration of phenolic compounds in fragments of algae submitted to herbivory than in fragments not submitted to herbivory (Van Alstyne 1988). In addition, shallowers waters may also present greater intensity of herbivory in relation to deeper waters (Hay 1981), which could also explain the higher concentrations of phenolics in turf samples from shallower depths.

Our results showed higher RC concentration in turf assemblages from warm temperate region, while phenolic compounds concentration was higher in extreme tropical region. The major ecological factors driving the production of primary and secondary metabolites were SST and PAR, the same determining large-scale patterns of turf-forming algae assemblages from Southwestern Atlantic. This leads us to understand that macroecological factors may not only determine the structuring of algae communities, but also the synthesis of their major categories of metabolites, as they represent a direct result of ecophysiological adaptations to environmental conditions.

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Compliance with Ethical Standards

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Ethical approval: This article does not contain any studies with animals performed by any of the authors.

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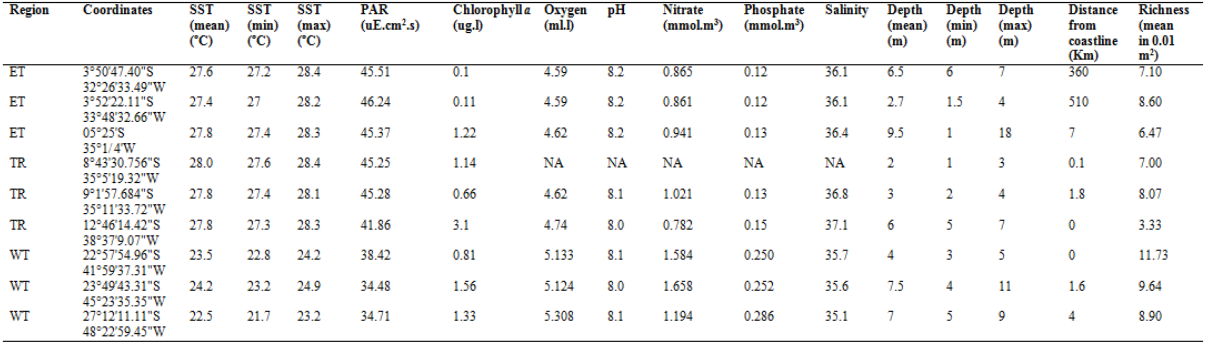
Supporting Information

Table S1: Sites where samples were collected and their corresponding region ("ET" for extreme tropical, "TR" for tropical and "WT" for warm temperate) and abiotic parameters (1) annual mean, minimum and maximum values of sea surface temperature (SST), (2) photosynthetically active radiation (PAR), (3) chlorophyll *a*, (4) oxygen, (5) pH, (6) nitrate, (7) phosphate and (8) salinity were extracted from MODIS Aqua Ocean Level-3 standard mapped archive products (Feldman & McClain 2012), produced and distributed by the NASA Goddard Space Flight Center's Ocean Data Processing System (ODPS) (data from 2003 to 2013); (9) means, minimum and maximum depths of sampling were taken *in situ*; (10) distance of each site from the coastline was calculated using satellite images taken from GoogleEarth®; (11) turf richness and (12) turf biomass data were taken from Martins et al. (*no prelo*)



Region	Coordinates	SST (mean) (°C)	SST (min) (°C)	SST (max) (°C)	PAR (uE.cm^2.s)	Chlorophyll *a* (ug.l)	Oxygen (ml.l)	pH	Nitrate (mmol.m^3)	Phosphate (mmol.m^3)	Salinity	Depth (mean) (m)	Depth (min) (m)	Depth (max) (m)	Distance from coastline (Km)	Richness (mean in 0.01 m^2)
ET	3°50'47.40"S 32°26'33.49"W	27.6	27.2	28.4	45.51	0.1	4.59	8.2	0.865	0.12	36.1	6.5	6	7	360	7.10
ET	3°52'22.11"S 33°48'32.66"W	27.4	27	28.2	46.24	0.11	4.59	8.2	0.861	0.12	36.1	2.7	1.5	4	510	8.60
ET	05°25'S 35°1/ 4'W	27.8	27.4	28.3	45.37	1.22	4.62	8.2	0.941	0.13	36.4	9.5	1	18	7	6.47
TR	8°43'30.756"S 35°5'19.32"W	28.0	27.6	28.4	45.25	1.14	NA	NA	NA	NA	NA	2	1	3	0.1	7.00
TR	9°1'57.684"S 35°11'33.72"W	27.8	27.4	28.1	45.28	0.66	4.62	8.1	1.021	0.13	36.8	3	2	4	1.8	8.07
TR	12°46'14.42"S 38°37'9.07"W	27.8	27.3	28.3	41.86	3.1	4.74	8.0	0.782	0.15	37.1	6	5	7	0	3.33
WT	22°57'54.96"S 41°59'37.31"W	23.5	22.8	24.2	38.42	0.81	5.133	8.1	1.584	0.250	35.7	4	3	5	0	11.73
WT	23°49'43.31"S 45°23'35.35"W	24.2	23.2	24.9	34.48	1.56	5.124	8.0	1.658	0.252	35.6	7.5	4	11	1.6	9.64
WT	27°12'11.11"S 48°22'59.45"W	22.5	21.7	23.2	34.71	1.33	5.308	8.1	1.194	0.286	35.1	7	5	9	4	8.90

Table S2: Sites and regions ("ET" for extreme tropical, "TR" for tropical and "WT" for warm temperate) where samples were collected and their corresponding concentration of total soluble sugar, total reserve carbohydrate and phenolic compounds

Site	Region	Total Soluble Sugar mg/g DW	Reserve Carbohydrate mg/g DW	Phenolic Compounds mg/g DW
Fernando de Noronha	ET	0.09 ± 0.04	5.40 ± 2.02	0.20 ± 0.14
Atol das Rocas	ET	0.20 ± 0.25	0.41 ± 0.25	0.05 ± 0.02
Natal	ET	0.15 ± 0.06	2.55 ± 2.27	0.67 ± 0.45
Tamandaré	TR	0.11 ± 0.06	1.99 ± 0.28	0.03 ± 0.01

Maragogi	TR	0.14 ± 0.07	2.31 ± 1.08	0.02 ± 0.01
Salvador	TR	0.14 ± 0.12	0.64 ± 0.25	0.03 ± 0
Arraial do Cabo	WT	0.26 ± 0.17	2.42 ± 0.75	0.08 ± 0.07
Ilhabela	WT	0.02 ± 0.01	10.91 ± 3.23	0.04 ± 0.02
Florianópolis	WT	0.21 ± 0.15	1.86 ± 0.58	0.07 ± 0.05

CONCLUSÃO GERAL

Diante dos resultados apresentados ao longo dos três capítulos desta tese, é possível concluir que a composição da estrutura da comunidade, assim como a síntese de metabólitos primários e secundários em macroalgas marinhas, são função do estado ecofisiológico da comunidade como um todo e estes processos são regulados por estressores que variam em diferentes escalas. Localmente destacam-se os nutrientes inorgânicos dissolvidos na água do mar, os quais podem variar nesta escala de forma significativa. Já em escalas regionais observam-se variações latitudinais de estressores abióticos e bióticos. Dentre os fatores abióticos, a temperatura da água e a radiação fotossinteticamente ativa que incide sobre o bentos, e dentre os bióticos, a competição e a herbivoria representariam os principais fatores que influenciam os padrões macroeclógicos do metaboloma e da estrutura da assembleia do turf.

Com base nos resultados obtidos no Capítulo 1, é possível afirmar que a riqueza e a abundância de metabólitos primários e secundários produzidos por comunidades de macroalgas marinhas é maior em ambientes cuja diversidade de espécies também é maior. Estes ambientes que apresentam maior riqueza e abundância de espécies correspondem a áreas com pouco ou nenhum impacto de origem antrópica, contrapondo áreas expostas a descargas de efluentes domésticos ou industriais, que apresentam concentrações extremamente altas de nutrientes inorgânicos dissolvidos, além de pouca ou nenhuma cobertura vegetal em áreas costeiras adjacentes. Os padrões observados por este trabalho representam argumentos consistentes para a intensificação de discussões acerca do manejo costeiro, com o objetivo de ampliar a conservação de áreas com alta diversidade ecológica e, conseqüentemente, do potencial biotecnológico que esses organismos podem representar. A partir das investigações propostas pelo Capítulo 2, é possível concluir que as assembleias de turf apresentam maior abundância na região tropical da costa oeste do Atlântico Sul e são majoritariamente dominadas por algas calcárias articuladas, especialmente *Jania* sp. e *Amphiroa* sp. A explicação mais plausível para este padrão combina estratégias adaptativas por parte das espécies dominantes para evitar herbivoria, especialmente em áreas tropicais, onde as interações biológicas são mais intensas, e para tornar seu desempenho ecofisiológico mais eficiente frente às condições ambientais a que estão expostas. Os fatores ambientais determinantes para a estruturação das assembleias de turf ao longo do gradiente latitudinal analisado foram a temperatura da superfície do mar (SST) e a radiação fotossinteticamente ativa (PAR). Estes dois fatores macroecológicos também foram os principais responsáveis por conduzir a produção de açúcares, carboidratos de reserva e compostos fenólicos, conforme demonstrado pelo Capítulo 3. Os resultados apresentados por este capítulo indicam maior concentração de carboidratos de reserva em assembleias de turf da região temperada quente, enquanto as maiores concentrações de compostos fenólicos foram encontradas nas assembleias da região extremo tropical. Esse padrão pode ser atribuído a estratégias adaptativas desenvolvidas pelas macroalgas para melhorar sua eficiência fotossintética, bem como para diminuir sua palatabilidade frente a herbívoros e seus danos oxidativos causados pela incidência de irradiação UV. Em síntese, os resultados deste trabalho confirmam que os fatores preditores dos padrões de diversidade das comunidades de macroalgas, sejam elas formadoras de dossel ou formadoras de turf, são também preditores da expressão metabólica de seus organismos constituintes.