2013-11

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<http://hdl.handle.net/10026.1/2888>

10.1016/j.marpolbul.2013.09.019

Marine Pollution Bulletin

Elsevier BV

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Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Coastal urbanization leads to remarkable seaweed species loss and community shifts along the SW Atlantic

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ARTICLE INFO

Keywords:

Phycogeographical regions

South-West Atlantic

Marine biodiversity loss

Urbanization metrics

Macroalgae

Calcareous algae

ABSTRACT

Coastal urbanization is rapidly expanding worldwide while its impacts on seaweed communities remain poorly understood. We assessed the impact of urbanization along an extensive latitudinal gradient encompassing three phycogeographical regions in the SW Atlantic. Human population density, number of dwellings, and terrestrial vegetation cover were determined for each survey area and correlated with diversity indices calculated from seaweed percent cover data. Urban areas had significantly lower calcareous algal cover (−38%), and there was significantly less carbonate in the sediment off urban areas than off reference areas. Seaweed richness averaged 26% less in urban areas than in areas with higher vegetation cover. We observed a remarkable decline in Phaeophyceae and a substantial increase of Chlorophyta in urban areas across a wide latitudinal gradient. Our data show that coastal urbanization is causing substantial loss of seaweed biodiversity in the SW Atlantic, and is considerably changing seaweed assemblages.

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1. Introduction

Coastal urbanization is rapidly advancing on a global scale, although relatively pristine areas still remain in South America. Terrestrial vegetation cover is being cleared and replaced with impervious surfaces, such as tarmac and concrete (Yuan and Bauer, 2007); in combination with human population growth this is increasing the run-off of contaminated waters into coastal seas (Marsalek et al., 1999; Bay et al., 2003). Almost 60% of the human population now lives within 100 km of the coasts, adversely affecting the oceans' productive coastal margins (Vitousek et al., 1997; Lotze et al., 2006; Worm et al., 2006; Halpern et al., 2008) and reducing the health of marine coastal ecosystems (Halpern et al., 2012). Marine biodiversity losses and community shifts are among the effects of coastal pollution. Such effects on seaweed communities have been documented worldwide; however, most studies have been designed to detect local impacts (i.e. Terlizzi et al., 2002; Oliveira and Qi, 2003; Liu et al., 2007; Martins et al., 2012). Assessments of the impact of urbanization on seaweed

communities at continental scale, and encompassing regions with different phycogeographical characteristics, are lacking.

Seaweeds are important coastal primary producers. Together with seagrasses they underpin many of the goods and services provided by coastal environments (Beaumont et al., 2007; Harley et al., 2012), providing habitat, nursery and food for marine fauna (Grall et al., 2006), removal of organic and inorganic pollutants from seawater (Wang and Zhao, 2007) and sequestering carbon (Koch et al., 2013). Furthermore, seaweed provides food for humans and has a variety of biotechnological applications in medicine, the food industry, agriculture, cosmetics and animal food (Zemke-White and Ohno, 1999). Calcareous algae, such as *Halimeda* and *Corallinaceae* provide essential ecological services in the marine environment, particularly in coral reef ecosystems where they play an important role in the carbon and carbonate budgets (Littler and Littler, 1988; Sinutok et al., 2012). However, calcareous algae and phaeophyceae species are very sensitive to pollution, while other seaweed groups, such as chlorophyta benefit from it (e.g. Bjork et al., 1995; Liu et al., 2009; Teichberg et al., 2010; Scherner et al., 2012a). Phaeophyceae species are known to have their reproduction and physiology negatively affected by urban pollution (Kevekordes, 2001; Scherner et al., 2012a), and calcareous algae

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may experience the negative effects of excess nutrients (Bjork et al., 1995), leading to declines in calcium carbonate productivity (Hallock and Schlager, 1986). The distinct responses of different phyla, functional groups, genera and species to coastal urbanization may cause substantial seaweed communities shifts, from perennial to ephemeral species' dominated systems, and a consequent decline in biodiversity.

The Brazilian coast is almost 8000 km long with a diverse set of oceanographic and ecological conditions (Floeter et al., 2006). The coast is divided into three major Phycogeographical Regions (PRs); the warm temperate province, the transition zone, and the tropical province (Horta et al., 2001). These PRs present differences in the seaweed flora that are thought to be mainly due to differences in substratum availability and seawater temperature. These different biogeographic conditions and the rapid coastal urbanization process observed along the coast makes it a natural laboratory to study the effects of urbanization on different seaweed communities, considering that effects may vary according to the environmental factors controlling the distribution of seaweed species, component of each PR. Against this background, we assessed the effects of coastal urbanization on different seaweed communities in the south-western Atlantic. We expect that intensive urbanization causes substantial seaweed species declines within all PRs, particularly among phaeophyceae and calcareous algae, and declines in carbonate in the sediment due to lower calcium carbonate productivity. It should reflect the lower water quality in urban areas, as assessed here by chlorophyll *a* concentrations. We tested the hypotheses that intensive coastal urbanization leads to: 1. lower water quality; 2. seaweed diversity declines; 3. declines of calcareous algae richness and cover; 4. lower carbonate in the sediment; 5. changes in seaweed species and phyla composition and percent cover within PRs.

2. Materials and methods

2.1. Study area

The occurrence of reefs is widespread along the coast occurring at least on a third of the coastline with coral reefs predominating in the north (0°52'N–19°S) and rocky reefs in the south (20–28°) (Floeter et al., 2006). The seawater temperature increases towards the north with average surface temperatures of 24 °C off São Paulo and Espírito Santo in the southeast region, and 28 °C off the coast of Pernambuco in the northeast (Fig. 1). The coast of Espírito Santo is influenced by low temperature, nutrient-rich upwelled water derived from an upwelling zone.

Most of the seventeen Brazilian coastal states have their capitals near the coast. Even when the capital is not located on the coast, large cities have grown, such as the Baixada Santista metropolitan area, on the coast of São Paulo with a population of 1.7 million. In Espírito Santo the coastal urban sprawl around Vitória also has 1.7 million people whereas in the north-eastern state of Pernambuco, Recife and neighboring cities have 3.7 million people (IBGE, 2010). In addition, there are medium sized coastal cities with relatively high numbers of dwellings, which increase in population density due to tourism in the holidays and summer months.

The Archipelago of Fernando de Noronha, (3°54'S–32°25'W), lies 360 km offshore and comprises 21 islands, covering 26 km². Average seawater surface temperature is around 28 °C yearly. The archipelago has 3500 inhabitants all concentrated on the main island. Since 1988, 2/3 of its terrestrial territory is protected as a National Park and the remaining territory is populated with restrictions as an Environmental Protection Area. Thus, urbanization on the archipelago is very low, especially along the coast.

2.2. Sampling design

Sampling design was planned to represent areas under high and low urban pressure. The coasts of the states of São Paulo, Espírito Santo and Pernambuco, and the archipelago of Fernando de Noronha, were surveyed, representing the warm temperate, the transition zone, and the tropical PRs, in the last case including the main land and an oceanic island, respectively (Fig. 1). Surveys were performed once at each sampling area during the summers of 2011 and 2012. A total of 25 areas were selected along the Brazilian coast and in the archipelago of Fernando de Noronha. The areas were selected based primarily on aspects that determine urban centres. The main parameters used to determine urban areas were: human population density, number of dwellings and vegetation index (Normalized Difference Vegetation Index – NDVI). Population and dwellings data were obtained from the 2010 census of the Brazilian Institute of Geography and Statistics (IBGE, 2010). To have an accurate picture of the sampling areas individually, a circumference of 2 km radius was generated from each sampling area using GIS techniques, and the urbanization parameters mentioned above were acquired only for the areas within the generated perimeters. Urban areas were considered those with number of dwellings and population above 7000 within the 2 km perimeters. Areas presenting values below those were considered areas under low urban pressure, and here they will be designated as reference areas. Additionally, sampling area selection criteria considered the homogeneity of environmental factors among areas, such as vertical inclination of substrata and salinity variations, avoiding estuaries and mangrove areas.

Seven areas were selected along the warm temperate province among which three were located in urban centres and four in reference areas. Along the transition zone nine areas were chosen of which four were located in urban centres and five in reference areas. Finally, nine areas were selected in the tropical province, three urban areas located in the continent and another six reference areas of which three were in the continent and the other half in the archipelago of Fernando de Noronha. Table 1 presents a summary of urban parameters of study areas.

Seaweed assemblages were quantitatively assessed on the lower intertidal zone, during low spring tides, using photoquadrats (625 cm²). This allowed standardization and sampling on the richest intertidal zone. In each area three sub areas 50 m apart were sampled and considered as triplicates. A thirty meter transect was positioned parallel to the shore and thirty photographs were taken in each sub area, one every meter, along the transect. Photographs were taken with a digital camera Canon G12 (Canon, Japan). A qualitative survey was carried out to identify the taxa present in each area and give taxonomic support to the photogeographical analysis. Seaweed were identified at the most detailed taxonomic level that could be achieved; some algae were grouped in the morpho-functional categories of Steneck and Dethier (1994). Nomenclature followed Wynne (2011).

Sediment samples were collected from the lower intertidal zone of the nearest available sandy substrata using a tubular core (8 cm diameter and 3.5 cm height). Three replicates were collected – approximately 30 m apart from each other.

2.3. Terrestrial vegetation cover

Normalized Difference Vegetation Index (NDVI) values were calculated using Resource-Sat-1 images with sensor LISS3 spanning the periods from 2011 to 2012 for the continent, and CBERS images from the CCD camera from 2007 for the archipelago of Fernando de Noronha. The images were rectified to the UTM projection system and were georeferenced onto a Brazilian Institute of Geography and Statistics (IBGE) base map.

Fig. 1. Surveyed locations along a latitudinal gradient in the south-west Atlantic (▼ = Urban areas; ▲ = Reference areas).

Normalized difference vegetation index maps were derived for all the images as follows:

$$NDVI = \frac{R_{NIR} - R_{red}}{R_{NIR} + R_{red}}$$

where R_{NIR} and R_{red} are the near-infrared and the red spectral reflectance, respectively. This equation generates values in the range from -1 to 1. Negative values approaching -1 correspond to water. Values close to zero generally represent non-vegetated surface such as rock and sand. Low positive values indicate grassland and shrub, while high values correspond to dense forests. Here, to avoid bias, negative values were not considered for analysis.

A total of 200 random points were plotted within 2 km range from each sampling area. The NDVI value of a pixel under each point was acquired, resulting in a table of 200 NDVI values. Their average value was used for statistical analysis. GIS procedures were performed using Quantum GIS 1.8.0 (Quantum GIS Development Team, 2012).

2.4. Sediment analyses

Sediment samples were transported to the laboratory in polyethylene bags and stored at 4 °C. Granulometric analyses were performed using a standard sieve (2 mm–63 µm) and pipette techniques (<63 µm). Carbonate (CaCO_3) content was estimated by weight difference after HCl 1N addition.

2.5. Water quality

Chlorophyll *a* is considered a key variable to be applied as a trophic state indicator and water quality (Boyer et al., 2009). It reflects the effect of multiple water quality factors that may be related to urbanization. Additionally, chlorophyll *a* data is available for a wide spatial range worldwide, which makes it relatively easy to acquire. For these reasons it was used here as an indicator of water quality. Chlorophyll *a* temporal mean concentrations (mg/m^3) from monthly climatologies (2002–2009) were obtained from

Table 1

Study areas, their locations, classifications, and urban parameters determined within a perimeter of 2 km from each study area.

Study area	Coordinates	Status	Phycogeographical Region	Population density	Dwellings	NDVI
Itamaracá	(−7.7841, −34.8356)	Urban	Tropical	907	7248	0.29
Pina	(−8.0899, −34.8805)	Urban	Tropical	23471	22843	0.01
Piedade	(−8.1775, −34.9161)	Urban	Tropical	19340	40747	0.02
Ponta de Pedras	(−7.6221, −34.8072)	Reference	Tropical	3707	2996	0.31
Itapoama	(−8.2992, −34.9513)	Reference	Tropical	314	3128	0.38
Muro Alto	(−8.4360, −34.9791)	Reference	Tropical	16	259	0.31
Praia do Leão	(−32.4406, −3.8712)	Reference	Tropical	359	660	0.67
Praia do Porto	(−32.4028, −3.8349)	Reference	Tropical	305	831	0.58
Caieira	(−32.3985, −3.8377)	Reference	Tropical	305	831	0.58
Ilha do Boi	(−20.3092, −40.2789)	Urban	Transition zone	16149	15580	0.07
Ilha do Frade	(−20.3030, −40.2808)	Urban	Transition zone	18705	17847	0.04
Praia da Costa	(−20.3336, −40.2734)	Urban	Transition zone	23822	14860	0.12
Castanheiras	(−20.6778, −40.5016)	Urban	Transition zone	7735	20092	0.17
Coqueiral de Aracruz	(−19.9203, −40.1019)	Reference	Transition zone	427	1160	0.45
Enseada das Garças	(−20.0307, −40.1586)	Reference	Transition zone	139	918	0.33
Castelhanos	(−20.8126, −40.6349)	Reference	Transition zone	2510	3326	0.32
Bacutia	(−20.7352, −40.5318)	Reference	Transition zone	924	4236	0.27
Parati	(−20.8029, −40.5986)	Reference	Transition zone	405	1646	0.29
Perequê Açú	(−23.4257, −45.0645)	Urban	Warm temperate	1477	11548	0.23
Ilha Porchat	(−23.9754, −46.3719)	Urban	Warm temperate	34324	36043	0.11
Praia da Costa	(−23.9784, −46.3858)	Urban	Warm temperate	30922	35473	0.09
Jurêia	(−23.5158, −45.1665)	Reference	Warm temperate	16	1529	0.60
Praia Branca	(−23.7649, −45.7860)	Reference	Warm temperate	273	1891	0.51
Praia Preta	(−23.8660, −46.1357)	Reference	Warm temperate	61	999	0.55
Praia Preta	(−23.8748, −46.1394)	Reference	Warm temperate	61	999	0.56

Bio-ORACLE dataset (Tyberghein et al., 2012). Three values closest to each survey area were acquired and used as triplicates for water quality analysis.

2.6. Seaweed percent cover and ecological indices determination

Photoquadrats were analyzed using Coral Point Count with Microsoft Excel extensions (CPCe; Kohler and Gill, 2006). Fifty random points were placed on each digital photoquadrat image. Identified seaweed species or functional groups occurring under each point allowed estimation of percent cover. Most macroalgae were identified to species, although a few taxa could only be identified to genus or family level. Turf algae and crustose coralline were lumped into functional groups. Percent cover of species that present any level of calcification (i.e. *Padina* spp., *Galaxaura* spp., *Hali-medea* spp., geniculate and crustose coralline) were selected to check for the effect of urbanization on their abundance.

Percent cover data were used to calculate species richness, Shannon–Wiener index (H'), and Pielou evenness (J). These indices are commonly used to assess anthropogenic impacts on marine communities (Johnston and Roberts, 2009). For these calculations data from each transect were treated as replicates, thus three values of each ecological index were obtained for each area. The indices were calculated using the software PRIMER Version 6 Beta (Plymouth Marine Laboratory, UK).

2.7. Statistics

Univariate analyses were used to test the hypothesis that urbanization causes seaweed diversity declines, assessing the relationship between ecological indices and urbanization within the different PRs. Normality and homogeneity of variances were previously evaluated using the Chi-square and Cochran tests, respectively, and when assumptions were verified parametric statistics was applied. The hierarchical nested ANOVA was performed to test for overall significant differences between urban and reference areas (nested within PRs) within the different PRs, using subareas as replicates ($n = 3$). Analyses were also carried out without the tropical oceanic island areas to test for a possible bias caused by

an eventual inflated diversity in the islands. Pearson's correlation analysis was used to examine the relationship between ecological indices and the different urban parameters described above.

Due to the non-parametric nature of calcareous algae percent cover, carbonate-sediment data, and Chlorophyll *a* values, the Mann–Whitney's U test was used to test for differences in these variables between urban and reference areas. The Kruskal–Wallis H test was used for comparisons among PRs. MANOVA was performed for granulometric data. All univariate procedures were performed using the data analysis software system STATISTICA 7.0 (StatSoft Inc., 2004).

Multivariate analyses were performed to test the hypothesis that intensive urbanization leads to changes in seaweed species and phyla composition and percent cover within the different PRs. Nested analyses were performed using quantitative and qualitative data (urban condition nested within PRs), using the software PRIMER 6.1.15 & PERMANOVA 1.0.5 (PRIMER-E Ltd., Plymouth Marine Laboratory, Plymouth, United Kingdom). A Bray–Curtis dissimilarity matrix was generated using all samples with square root transformed data (Clarke and Warwick, 1994). Qualitative analysis was performed using Sorensen's coefficient. Percent cover and qualitative data obtained at each sub area was treated as individual replicate. Nonmetric Multidimensional Scaling (nMDS) graphics were created to depict relationships among the studied areas. The percent contribution by individual species to differences in community assemblages between urban and reference areas were determined using Similarity Percentages – species contribution (SIMPER) (Clarke, 1993).

Table 2Summary of Mann–Whitney's U test and Kruskal–Wallis H test for the effects of urbanization and Phycogeographical Regions (PRs), respectively, on sediment carbonate, chlorophyll *a* and calcareous algae percent cover.

Source of variation	Urbanization				PRs		
	df	U	Z	p	df	H	p
Carbonate	1	465	−2.27	<0.05	2	40	<0.0001
Chlorophyll <i>a</i>	1	474	2.17	<0.05	2	46	<0.0001
Calcareous algae	1	460	−2.32	<0.05	2	30	<0.0001

Table 3

Summary of hierarchical nested ANOVA for the effects of Phycogeographical Regions (PRs) and urbanization (nested within PRs) on ecological indices.

Source of variation	df	Mean-square	F	p
<i>Species richness</i>				
PRs	2	227.12	12	<0.0001
Urbanization (PRs)	3	209.1	11.04	<0.0001
Error	69	18.92		
<i>Shannon–Wiener</i>				
PRs	2	1.71	11.39	<0.0001
Urbanization (PRs)	3	0.96	6.41	<0.001
Error	69	0.15		
<i>Pielou evenness</i>				
PRs	2	0.07	6.33	<0.005
Urbanization (PRs)	3	0.02	2.07	NS
Error	69	0.01		

3. Results

3.1. Sediment characterization

Percentage of carbonate in sediment was significantly different between urban and reference areas and among PRs (Table 2). Among PRs, significant higher average percent values were observed in the tropical region (52.2) and transition zone (30.8), compared to the warm temperate region (4.0) ($p < 0.0001$). A decline of 58% on the average percent values of carbonate was observed in urban areas compared to reference areas (17.5 and 42.4, respectively). There were no significant differences in granulometry between urban and reference areas (MANOVA, $F = 1.09$; $p < 0.38$).

3.2. Water quality

Chlorophyll *a* concentrations were significantly higher in urban areas than in reference areas (Table 2), averaging ($\pm$ SE) 2.8 ± 0.5 and 1.8 ± 0.3 mg/m³ in urban and reference areas, respectively. Significant differences were observed among PRs (Table 2). The *Post Hoc* test showed significant lower average values ($\pm$ SE) observed in the tropical region 0.8 ± 0.2 , comparing to the transition zone 3.3 ± 0.3 ($p < 0.0001$) and the warm temperate region 2.5 ± 0.4 ($p < 0.0001$). No differences were observed between the last two PRs.

3.3. Seaweed community

3.3.1. Calcareous algae

A significant reduction of 38% on average percent cover of calcareous algae was observed in urban areas comparing to reference

areas as indicated by Mann–Whitney's U test (Table 2). Such declines were observed with different intensities within all PRs (95% tropical; 68% warm temperate; 10% transition zone). In reference areas calcareous algae represented 21% of the total algal cover while fleshy algae corresponded to 79%. In urban areas calcareous algae represented 13% of the total cover. Significant differences were observed among PRs (Table 2). The *Post Hoc* comparison test shows significant higher percent cover values for the transition zone comparing to the other PRs ($p < 0.0001$).

3.3.2. Ecological indices

The average number of species occurring in urban areas ($15 \pm$ SE 1.4, $n = 10$) was significantly lower than the average number observed in reference areas ($20.3 \pm$ SE 1.1, $n = 15$) (Table 3), representing a difference of 26%. The same pattern was observed for species richness and Shannon–Wiener index, while Pielou evenness presented no significant differences between urban and reference areas (Fig. 2). Exclusion of the oceanic island from the analyses provided the same patterns described above with similar levels of significance, indicating no data inflation due to the inclusion of the archipelago in the sampling design. Mean values of ecological indices for each area and the summary of ANOVA for analyses carried out without islands are available as Supplementary data (Tables A1 and A2).

Species richness presented significant negative correlations with population density and number of dwellings, and significant positive correlations with vegetation index (Fig. 3). Although with lower correlation coefficients, significant negative correlation was observed for Shannon–Wiener index for the first two parameters, while a positive correlation was detected for vegetation index. Pielou evenness did not present significant correlation with any of the urbanization aspects assessed.

3.3.3. Seaweed assemblage patterns

A qualitative analysis of Rhodophyta, Chlorophyta and Phaeophyceae indicates significant differences between urban and reference areas, but not among PRs (Table 4). The percent cover of higher groups differed significantly between urban and reference areas, and among PRs (Table 4). The results show an increase of Chlorophyta and a reduction of Rhodophyta and Phaeophyceae percent cover in urban areas. However, changes on percent cover of higher groups did not occur within all PRs (Fig. 4). Pair-Wise comparison tests indicate that these shifts were observed within the tropical and warm temperate regions but not within the transition zone (Table 5). According to SIMPER, the average percent abundance of higher groups were: 60.9, 18.4 and 17.5 in reference areas and 53.7, 35.0 and 9.4 in urban areas, for Rhodophyta, Chlorophyta and Phaeophyceae, respectively. The percent contribution

Fig. 2. Average values ($\pm$ SE) of ecological indices obtained from all urban and reference sampling areas along the south-west Atlantic from 2011 to 2012. Letters above bars indicate significant differences according to nested ANOVA ($n = 10$ urban areas; 15 reference areas).

Fig. 3. Correlations between ecological indices and the different urbanization parameters assessed ($n = 75$).

of these groups to differences in seaweed assemblages between urban and reference areas were, in that order: 38.6, 37.7 and 23.6.

A total of 192 seaweed taxa, including the two functional groups, occurred in the photoquadrats in all surveyed areas (a full species list is available as [Supplementary data – Table A3](#)). In urban

Table 4
Results of PERMANOVA for the effects of Phycogeographical Regions (PRs) and urbanization (nested within PRs) on seaweed communities.

Source of variation	df	Mean-square	Pseudo-F	p
<i>Phyla (% cover)</i>				
PRs	2	4268.5	2.51	<0.01
Urbanization (PRs)	3	1703	11.74	<0.005
Error	69	145		
<i>Taxa (% cover)^a</i>				
PRs	2	33347	2.32	<0.05
Urbanization (PRs)	3	14425	6.53	<0.0005
Error	69	2208.9		
<i>Taxa (qualitative)^a</i>				
PRs	2	36988	3.23	<0.05
Urbanization (PRs)	3	11498	6.82	<0.005
Error	69	1684.1		

^a Including functional groups.

areas a total of 102 taxa were observed while in reference areas it reached 169. Seaweed percent cover data provided significant differences between urban and reference areas within PRs and between PRs (Tables 4 and 5). Similarly, the qualitative analysis provided significant differences between urban and reference areas within PRs and between PRs (Tables 4 and 5).

The nMDS (Clarke and Warwick, 2001) based on seaweed percent cover (Fig. 5 a) and on qualitative data (Fig. 5 b) formed three main clusters due to dissimilarity among the PRs. Secondary clusters were formed within the main PR clusters, illustrating the dissimilarities between urban and reference areas within PRs, although this was more pronounced in the tropical and warm temperate regions.

SIMPER results show that the most abundant taxa in reference areas were: *Palisada perforata*, *Hypnea musciformis* and *Gellidiella acerosa*, while in urban areas the most abundant were *Ulva* spp., *Ceratodictyon planicaule*, *Chondracanthus acicularis* and *Colpomenia sinuosa*. Table 6 presents the taxa which most contributed to differences in seaweed assemblages between urban and reference areas with their corresponding contribution values and average abundance. The most abundant taxa varied greatly according to PRs. Within the tropical region *C. planicaule* and *P. perforata* were the most abundant in urban and reference areas, respectively. In the transition zone *Ulva* species, *C. sinuosa* and *Arthrocardia*

Fig. 4. Average ($\pm$ SE) percent cover of Rhodophyta, Chlorophyta and Phaeophyceae within the different phycogeographical regions (▲ = urban areas; $n = 3$, tropical; 4 transition zone; 3 warm temperate; ● = reference areas; $n = 6$, tropical; 5, transition zone; 4, warm temperate).

Table 5

Results of PERMANOVA Pair-Wise comparison tests for the effects of urbanization within the different Phycogeographical Regions (PRs) on seaweed communities.

PRs	Phyla (% cover)		Taxa (% cover) ^a		Taxa (qualitative) ^a	
	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>
Tropical	4.02	0.001	3.33	0.0001	2.84	0.001
Transition zone	0.22	0.946	1.89	0.0001	2.22	0.001
Warm temperate	5.04	0.001	2.34	0.0001	2.73	0.001

^a Including functional groups.

variabilis presented the highest abundance in urban areas followed by *P. perforata* in reference areas. Within the warm temperate region *Ulva* species were the most abundant in urban areas followed by *H. musciformis* in reference areas.

4. Discussion

Given the current exponential rate of coastal development along the SW Atlantic, there is an urgent need to survey its biodiversity (Turra et al., 2013). Such studies are important to give a dimension of the environmental changes caused by urbanization as to provide valuable information to forecast future changes, and thus, plan effective mitigation measures and conservation strategies. In this sense, this study is an effort to assess what is being lost due to urban pressures along the SW Atlantic coast.

Our data showed a marked reduction in calcareous algae accompanied by declines in sediment carbonate content in areas of high urban pressure. This is likely to be a result of nutrient enriched waters. Hallock and Schlager (1986) proposed the following reasons for why excess nutrients are detrimental to reef communities and calcium carbonate productivity: 1. Reduction in water transparency caused by increased phytoplankton growth; 2. phosphate inhibition of calcium carbonate crystal formation; 3. biotic disruption; and 4. increased bioerosion. Experiments in reef environments have shown that increased nutrients coupled with decreased grazing pressure results in increased dominance of fleshy macroalgae (Belliveau and Paul, 2002; McClanahan et al., 2003). Additionally, eutrophication of coastal waters increases acidity (Cai et al., 2011). Such local events have potential to act synergistically with global ocean acidification (Martin et al., 2008; Johnson et al., 2012; Roberts et al., 2013), accelerating the loss of calcareous organisms from nutrient-enriched areas (Anthony et al., 2011). Although we used chlorophyll *a* as an indicator of water quality, it is important to consider that a wide range of contaminants such as metals, polycyclic aromatic hydrocarbons (PAHs), and herbicides, with known deleterious effects to seaweeds, are often discharged into urban coastal areas (Hoffman et al., 1984; Pagliosa and Barbosa, 2006; Torres et al., 2008; Lewis et al., 2009).

The effects of urbanization on seaweed communities along the Brazilian coast presented reductions in biodiversity, as observed by reduced species richness and Shannon–Wiener index. However, no changes on dominance of species (i.e. Pielou evenness) were

Fig. 5. Non-metric multidimensional scaling (nMDS) of seaweed communities from urban and reference areas within the different phycogeographical regions studied. (a) Percent cover data; (b) qualitative data. Each marker represents a subarea.

observed as a consequence of urbanization. Previous studies have found similar results for intertidal communities (Johnston and Roberts, 2009). The seaweed diversity declines observed in our study were more closely related to richness reduction than to increased dominance of tolerant species. Insignificant changes in evenness indicate that the percentage of different species increased in similar proportions, as the number of species decreased.

The levels of significance and correlation strength between the urbanization aspects evaluated and the ecological indices assessed

here increased towards the indices that have a greater component of taxa number (i.e. in ascending order: Pielou evenness, Shannon–Wiener and species richness). The urbanization aspects that presented negative correlation with species richness and Shannon–Wiener index: population density and number of dwellings, indicate that intensive human occupation on coastal areas impacts significantly on seaweed diversity. Furthermore, it shows that even touristic areas with low resident population but that present substantial number of dwellings, used as weekend and summer homes, were subjected to seaweed diversity declines

Table 6

Taxa and functional groups which most contributed to the dissimilarities between urban and reference areas across and within each PR (calculated using similarities of percentages (SIMPER)). Only taxa and functional groups with contributions above or equal to 3% are presented.

	Average abundance		Average dissimilarity	Dissimilarity (SD)	Contribution (%)	Cumulative contribution (%)
	Reference	Urban				
All PRs						
<i>Ulva</i> spp.	6.57	22.44	11.25	0.99	12.39	12.39
<i>Palisada perforata</i>	15.63	1.86	7.94	0.72	8.74	21.13
<i>Ceratodictyon planicaule</i>	0.08	10.52	5.28	0.44	5.81	26.94
<i>Hypnea musciformis</i>	7.47	4.23	4.66	0.7	5.13	32.07
<i>Chondracanthus acicularis</i>	0	8.6	4.3	0.55	4.73	36.81
<i>Colpomenia sinuosa</i>	1.61	5.3	2.93	0.68	3.23	40.03
<i>Gelidiella acerosa</i>	5.17	0.69	2.73	0.6	3	43.04
Tropical						
<i>Ceratodictyon planicaule</i>	0.21	35.05	17.44	1.08	19.2	19.2
<i>Palisada perforata</i>	32.71	5.83	15.05	1.26	16.57	35.77
<i>Chondracanthus acicularis</i>	0.01	27.82	13.9	1.68	15.31	51.08
<i>Hypnea musciformis</i>	10.62	7.85	7.16	0.85	7.88	58.96
<i>Gelidiella acerosa</i>	12.93	2.29	5.94	1.15	6.53	65.49
<i>Ulva</i> spp.	0.41	10.27	5.07	1.12	5.58	71.07
<i>Sargassum cymosum</i>	5.78	0	2.89	0.5	3.18	74.25
Transition zone						
<i>Ulva</i> spp.	19.51	7.43	10.1	1.03	12.47	12.47
<i>Colpomenia sinuosa</i>	13.26	4.71	5.16	1.1	6.37	18.84
<i>Arthrocardia variabilis</i>	8.66	3.83	5.1	0.79	6.3	25.13
<i>Palisada perforata</i>	0.29	7.62	3.77	0.72	4.66	29.79
Turf	4.54	7.17	3.42	0.68	4.22	34.01
<i>Ulva lactuca</i>	4.67	3.3	3.09	0.83	3.81	37.82
<i>Amphyroa anastomosans</i>	0.93	5.22	2.8	0.68	3.45	41.27
<i>Codium intertextum</i>	1.12	5.46	2.71	0.99	3.34	44.61
<i>Dictyota ciliolata</i>	0.93	4.44	2.49	0.48	3.08	47.69
Warm temperate						
<i>Ulva</i> spp.	14.74	38.52	17.08	1.44	20.14	20.14
<i>Ulva lingulata</i>	0	11.91	5.96	0.7	7.02	27.15
<i>Hypnea musciformis</i>	8.54	0.06	4.27	0.72	5.03	32.19
<i>Gymnogongrus griffithsiae</i>	0.13	8.5	4.22	0.72	4.97	37.16
<i>Chondracanthus teedei</i>	4.68	8.83	4.14	1.3	4.88	42.04
<i>Chondracanthus</i> sp.	7.75	0	3.87	0.85	4.57	46.61
<i>Acanthophora spicifera</i>	6.15	0.24	3.14	0.59	3.7	50.31
<i>Chaetomorpha</i> sp.	5.65	0.16	2.84	0.56	3.34	53.65
<i>Coralline algae</i>	5.42	0	2.71	0.97	3.19	56.85

(e.g. Itamaracá). Conversely, terrestrial vegetation (NDVI) presents positive correlations with these two indices. This is expected because generally highly urbanized areas have less vegetation cover, and although less urbanized areas may be deficient in vegetation for different reasons (i.e. mining, soil preparation for agriculture) which are not necessarily associated with urbanization, the reference areas chosen avoided areas with such activities. Because NDVI is negatively correlated with impervious surfaces (Carlson and Arthur, 2000) it provides a good indication of the potential of urban runoffs (Corbett et al., 1997) and thus, of the consequent contamination of the marine environment. Additionally, higher runoff volumes lead to increased variation in salinity (Scherner et al., 2012a), which has the potential to cause seaweed community shifts from perennial to ephemeral seaweed dominated systems (Scherner et al., 2012b).

Remarkable alterations were also observed in seaweed communities structure when considering different levels of taxonomic organization. The large declines of Phaeophyceae taxa observed in urban areas of tropical and warm temperate PRs was accompanied by a substantial increase in Chlorophyta taxa. This is in accordance with other studies which have reported the same pattern occurring in areas impacted by different anthropogenic activities (e.g. Oliveira and Qi, 2003). It occurs due to the sensitivity of most Phaeophyceae species to anthropogenic contaminants, from negative effects on germination and cell division (Kevorkides, 2001) to declines in photosynthetic performance (Scherner et al., 2012a), while numerous Chlorophyta species benefit from or are not negatively affected by such impacts (Tewari and Joshi, 1988; Liu et al., 2009; Teichberg et al., 2010; Scherner et al., 2012a). In contrast, higher groups' shifts were not observed between reference and urban areas within the transition zone. Among the Phaeophyceae it can be explained by a high contribution of *C. sinuosa* to urban areas within this PR, a species that has been previously associated to areas impacted by sewage (Terlizzi et al., 2002). However, in general, the singular characteristics of this region may have an important role on sustaining the observed patterns. This region presents characteristics that benefit seaweed species from both tropical and warm temperate regions; consequently presenting the richest seaweed flora on the southwestern Atlantic (Horta et al., 2001). It presents a diversity of habitats for colonization, and experience the influence of colder, nutrient-rich upwelled water derived from a neighbor upwelling zone of Cabo Frio, that favors seaweed growth.

The structure of seaweed communities represented by infra-generic taxa presented a clear pattern of segregation between urban and reference areas within their respective PRs. It indicates that the impacts of urbanization do not alter the phycogeographical character of seaweed communities, but causes shifts from sensitive to tolerant species dominated systems between urban and reference areas within PRs. Such shifts are related both to substantial declines of pollution-sensitive taxa such as *P. perforata*, *H. musciformis*, *Gelidiella acerosa* and Coralline species from reference areas and a profuse colonization of tolerant species such as *Ulva* spp., *C. planicaule*, *C. acicularis* and *C. sinuosa* in urban areas. These results are in accordance with previous studies (e.g. Terlizzi et al., 2002).

Large scale studies that employ multiple impacted and reference areas have power increased and thus are more likely to detect impacts (Underwood and Chapman, 2003). Here we have shown at a continental scale that urbanization leads to changes in seaweed assemblages, considerably reducing richness and percent cover of sensitive species, especially of calcareous algae and Phaeophyceae, as a consequence of declines in water quality (De'ath and Fabricius, 2010). The loss of primary producers is highly detrimental to the marine environment because it propagates through the food chain, causing dramatic loss of fauna at multiple levels and changing the trophic structure of marine communities (Airoldi et al., 2008;

Haddad et al., 2009). In this context, more efficient land use in urban areas is important to mitigate the impacts of coastal urbanization and human population growth on marine biodiversity (Sushinsky et al., 2013). Considering the results presented here and the current worldwide fast growing coastal urbanization process, public policies should consider a combination of expanded conservation efforts of coastal land-sea systems, and techniques to mitigate the contamination of the marine environment by anthropogenic pollutants in urban areas.

Acknowledgments

This study was funded by the Brazilian Coordination for the Improvement of Higher Level Personnel (CAPES), under the project PNADB No. 17/2009. Supplementary financial support was also provided by the Brazilian Marine Biodiversity Network – SISBIOT-Amar. Field and laboratorial work was performed with the valuable assistance of several collaborators from the University of São Paulo, the Federal Rural University of Pernambuco, the Federal University of Espírito Santo, and the Federal University of Santa Catarina.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.marpolbul.2013.09.019>.

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