

Gabriela Carvalho Lourenço da Silva

Scales of variation of subtidal benthic communities in islands within a marine protected area in SE Brazil: clues about structuring processes and subsidies for monitoring



São Paulo

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bentônicas de infralitoral em ilhas
pertencentes a uma área de proteção
ambiental no Sudeste do Brasil: reflexões
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“Necessito do mar porque me ensina:
não sei se aprendo música ou consciência:
não sei se é onda só ou ser profundo
ou somente rouca voz ou deslumbrante
suposição de peixes e navios.
O fato é que até quando estou dormindo
de algum modo magnético círculo
na universidade da ondulação.
Não são somente as conchas trituradas
como se algum trêmulo planeta
participara paulatina morte,
não, do fragmento reconstruo o dia,
de uma rajada de sal a estalactite
e de uma colherada o deus imenso.

O que antes me ensinou o guardo! É ar,
incessante vento, água e areia.

Parece pouco para o homem jovem
que aqui chegou a viver com seus incêndios,
e no entanto a pulsação que subia
e baixava a seu abismo,
o frio do azul que crepitava,
o desmoronamento da estrela,
o tenro desdobrar-se da onda
desperdiçando neve com a espuma,
o poder quieto, ali, determinado
como um trono de pedra no profundo,
substituiu o recinto em que cresciam
tristeza teimosa, amontoando esquecimento,
e mudou bruscamente minha existência:
de minha adesão ao puro movimento.”

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Resumo

Como os processos que definem distribuições de espécies operam em diferentes escalas espaciais, abordagens multi-escalares são necessárias para que a variabilidade do sistema seja considerada no desenvolvimento de desenhos amostrais. Estudos sobre padrões espaciais de distribuição são necessários para servir de base para monitoramento e avaliações de impactos. Este trabalho avaliou a variação espacial de comunidades de infralitoral, em costões rochosos de três ilhas na Estação Ecológica dos Tupinambás. Os padrões espaciais foram investigados em quatro escalas, que variam de poucos metros a dezenas de quilômetros. Foram amostradas as profundidades de 1 a 5 e de 5 a 10 metros, no verão e inverno de 2013 e verão de 2014. O recobrimento percentual das unidades biológicas foi extraído a partir de foto-quadrados de 50x50 cm, aleatorizados, seguindo um desenho amostral aninhado. Os dominantes foram analisados individualmente com análise de variância univariada. Algas Calcárias Articuladas (ACA) foram o grupo dominante em todas as ilhas, períodos e profundidades, além de influenciar padrões multivariados, evidenciados pelo PCA. O recobrimento médio de ACA variou de 36% a 89.56%, considerando toda a amostragem. Outros dominantes variaram de acordo com o período e profundidade de coleta, dentre eles, *Sargassum* sp., *Codium intertextum* e *Asparagopsis taxiformis*. Todas as análises multivariadas (PERMANOVA, Pairwise Comparisons e nMDS) revelaram alta variação entre ilhas. Todas as outras escalas apresentaram variabilidade significativa, exceto a de poucos metros. Estimativas de variação revelaram que a variação residual e a entre ilhas foram sempre maiores do que as das outras escalas, confirmando a heterogeneidade intrínseca em pequena escala e a complexidade de comunidades insulares. O monitoramento nesta UC deverá incorporar todas as escalas investigadas.

Abstract

As processes that define species distributions operate at different spatial scales, multi-scale approaches are needed to account for the system's natural variability, when developing sampling designs. Research about spatial patterns is essential to generate data to drive monitoring initiatives and impact assessments. The present study evaluated the spatial variability of subtidal rocky shore communities in three islands within the Ecological Station of Tupinambás. Spatial patterns were investigated across four scales, ranging from few meters to tens of kilometers, from 1 to 5 and from 5 to 10 m depth, in the summer and winter of 2013 and summer of 2014. Percent cover of the biological units was evaluated from photo-quadrats of 50x50 cm, randomly scattered, following a nested design. Dominant species and morphological groups were analyzed individually by univariate analyses of variance. Articulated Calcareous Algae (ACA) were the dominant group in all islands, depths and periods, and the main driver of multivariate patterns, as evidenced by the PCA. Mean cover of ACA varied from 36% to 89.56%, considering all occasions. Other dominant species were the algae *Sargassum* sp., *Codium intertextum* and *Asparagopsis taxiformis*, which varied according to sampling period and depth. All multivariate procedures (PERMANOVA, Pairwise Comparisons and nMDS plots) showed the highest variability among islands. All the other scales, except of few meters, presented significant variability. Estimates of variation showed that residual and intra-island variability were always higher than in other scales, confirming the intrinsic small-scale patchiness of marine assemblages and the complexity of insular communities. Monitoring efforts in this MPA should incorporate all the examined scales.

Introduction

Spatial scales and studies related

As marine systems are naturally variable, for many years, studying spatial heterogeneity has become a central problem in ecology. (Underwood & Chapman, 1996; Guichard & Bourget, 1998; Fraschetti *et al.*, 2005). The intrinsic heterogeneity within and among marine communities is a consequence of various processes, both physical and biological, that operate therein. As these processes operate on a range of spatial scales (Menge & Olson, 1990; Underwood, 1997), this hierarchical nature of spatial variability is an intrinsic property in many habitats (Benedetti-Cecchi, 2001). Spatial variation is organically and environmentally dependent, what hinders formulating generalizations about environments other than those investigated, thereby leaving information about particular environments yet to be gathered (Fraschetti *et al.*, 2005).

Spatial scales of variation are a reflex of the processes determining marine distribution. Knowledge on these distribution patterns allows for focusing on the relevant processes and the appropriate scales, when undertaking manipulative experiments (Underwood, 1997; Underwood *et al.*, 2000). Testing hypotheses regarding patterns with a sound experimental design is recognized as part of the experimental ecology spectrum, and comprises the primary base of observational studies (Underwood *et al.*, 2000). Without proper knowledge of the patterns time can be wasted on studying irrelevant processes (Underwood, 1997, Lourie & Vincent, 2004).

Knowledge on marine distribution provides specific information on conservation targets (ecosystems, species and genes), and forms the bases for biogeographic classification and monitoring initiatives (Lourie &

Vincent, 2004). Descriptive studies are also necessary precursors for manipulative experimental analysis. Furthermore, mapping unfamiliar habitats, such as marine insular environments, is a further requirement to ensure that these ecosystems are truly represented in Marine Protected Areas (Lourie & Vincent, 2004).

Despite the increasing number of studies involving multiple scales, both descriptive and experimental, the tropical environment remains widely understudied (but see Hutchinson & Williams, 2001; Cornell *et al.*, 2007; Entrambasaguas *et al.*, 2008; Huntington *et al.*, 2010; Martins *et al.*, 2012; Francini-Filho *et al.*, 2013; Scherner *et al.*, 2013). As regards the Brazilian coastal extent, the area that has been sampled to date is as yet extremely small. Generally speaking, archipelagos are understudied systems, especially as regards marine communities, which makes it difficult to correlate patterns with natural processes and make comparisons with other studies.

Researching these environments can be relevant for testing hypotheses about other fragmented systems, such as Marine Protected Areas (Martins *et al.*, 2008). In the Southeastern Brazil Ecoregion (Spalding *et al.*, 2007) data regarding benthic communities of Insular Marine Protected Areas is very scarce (but see Amado Filho *et al.*, 2006 and Ghilardi, 2007). The most limiting factors responsible for the small number of sampled area seems to be the methodologies applied, the difficulties inherent to working in the marine environment, and the need for students, researchers and technicians, capacitated in the field, particularly in the subtidal zone, the least studied region (Berchez *et al.*, 2005).

Threats to marine environments

This lack of previous data complicates impact detection, the evaluation of its extent and reaching predictions, when evaluating

consequences. This is of grave concern since it hinders the implementation of effective action for their mitigation and compensation (Ghilardi *et al.*, 2008). Even in well-replicated studies, lack of baseline data is a challenge to the evaluation of management effects in protected areas, by confusing these with differences in seascape variation (Huntington *et al.*, 2010).

On a global scale, no area in the marine environment is absolutely free from human influence (Halpern *et al.*, 2008). Coastal areas are severely subjected to pressure from human activities (Oliveira *et al.*, 2014), and global changes have already been observed and predicted for such environments (Field *et al.*, 2007), such as biodiversity loss and alterations in the composition and distribution of ecosystems (Magrin *et al.*, 2007; Turra *et al.*, 2013). The study region is the most rapidly developing area in the state, and SW Atlantic rocky shores are already undergoing immediate damage-pressure, thus facing many threats to marine biodiversity (Turra *et al.*, 2013; Leite, 2014).

Theoretical studies, such as those of metapopulations, have already evaluated anthropic pressure, pointing out that habitat loss due to area reduction, fragmentation or deterioration is an extremely important factor in species decline. However these models only include major simplification, hence there is still a lot to be studied (Sih *et al.*, 2000). Meanwhile, many studies are already testing the effects of anthropogenic impacts on the biota in order to formulate predictions and possibly mitigate such disturbances. Extensive evidence shows that global environmental changes are affecting both the quality and the quantity of marine ecosystems' goods and services (Turra *et al.*, 2013).

Impacts related to coastal urbanization are frequently observed in marine systems. Local factors, such as water turbidity, hydrodynamic modification, chemical pollution and inputs of dissolved nutrients and suspended particular material, can drastically alter patterns of abundance

and distribution in benthic organisms, both independently and coupled with natural disturbances (Oliveira *et al.*, 2014, and references therein). Anthropogenic impacts are also known to reduce diversity and affect the balance and resilience of communities (Martins *et al.*, 2012). Studies revealed considerable loss of seaweed biodiversity, as well as changes in assemblages, as a result of coastal urbanization and the deterioration in water quality (Schermer *et al.*, 2013; Oliveira *et al.*, 2014). In the SW Atlantic, Scherner *et al.* (2013) observed declines in sediment carbonate content and calcareous algae abundance, due to nutrient enrichment. Mussel fisheries, an activity which is also intensively practiced in this region, was found to reduce the mean number of taxa in the Mediterranean, thereby homogenizing assemblages and, compromising primary and secondary production on rocky reefs (Bevilacqua *et al.*, 2006). These are some of the many examples of anthropogenic threats to marine communities.

The effects of climate change can also affect marine communities. Extreme climate events, for example, are predicted to increase in frequency and intensity, as a result of global warming (Wernberg *et al.*, 2012). Increasing temperatures have been related to both carbon emission, which furthers ocean acidification (Johnson & Carpenter, 2012), as well as meteorological instability, with the consequential increase in erosion and the appearance of storms surges and alteration of precipitation regimes, simultaneous with other effects, such as sea level rising (Hubbard *et al.*, 2014). Linking particular events with long-term climate change and human influence requires caution (Kerr, 2013). For all that, improved models are constantly being developed to forecast possible scenarios. Many researchers are testing the effects of climate change on the biota based on these predictions, and also evaluating the response of communities to occurring climate events.

Heat waves have caused a significant reduction in habitat-forming seaweeds, and given rise to depauperation of community structures in Australia (Wernberg *et al.*, 2012). Wind intensification has been observed in many upwelling systems at high latitudes. This can result in warming trends towards the pole. Nonetheless, forecasting consequences is complex. Although ocean warming may result in stronger upwelling, thence enhancing nutrient input in subtropical systems, it may also act otherwise by enhancing stratification and disrupting trophic interaction (Sydeman *et al.*, 2014). Ocean acidification and warming have negative effects on calcifying organisms such as coralline algae and corals. Furthermore, the synergistic effects of these factors complicate long-term prediction. Even so, evidence has shown that a decrease in calcification rates increases coralline algae susceptibility to grazing, with the consequential cascading effects and major implications to community structures (Johnson & Carpenter, 2012).

Especially for Latin America, the effects of climate change, such as changes in the composition and distribution of sensitive habitats, bleaching and diseases in coral reefs, and the increase in extreme events, have already been observed (Turra *et al.*, 2013, and references therein). Other than that, predictions are under way about the effects on marine systems of changes in temperatures and currents, ocean acidification and harmful algal blooms, all of which resulting in critical impacts on human populations (Turra *et al.*, 2013). Unfortunately, effects on Latin American coastal habitats still remain understudied, thus seriously compromising forecasting. Habitat evaluations are scattered and the divergent methodologies applied complicate data unification (Magrin *et al.*, 2007; Turra *et al.*, 2013). Thus, an understanding of the effects of global environmental change is essential for providing early warning systems and preparing society for coping with changes (Turra *et al.*, 2013).

Conservation Units and Monitoring

The establishment of conservation units has increased over the past decade (Huntington *et al.*, 2010). Apart from conservation, they are also useful as reference sites for research and environmental monitoring (Leite, 2014). Full protection areas, including marine reserves, comprise one of the few management tools available to mitigate the effects of large-scale environmental impacts (Micheli *et al.*, 2012). For example, Marine Protected Areas (MPAs) are known to increase density, biomass, individual size and diversity of many functional groups (Bevilacqua *et al.*, 2006). Furthermore, experimentation with a number of stress factors has shown that MPAs facilitate assemblage recovery, and resistance to climate change and anthropogenic impacts. Even more, protection was found to enhance resilience, both in benthic assemblages through the indirect effects of recolonization (Bevilacqua *et al.*, 2006), and in fish through the maintenance of higher larval production and recruitment (Micheli *et al.*, 2012).

In the year of 2000, the Brazilian, National System of Conservation Units (SNUC) was founded, thereby establishing criteria for the implementation and management of conservation units in the countrywide. As this system was idealized as a management tool for terrestrial environments, its' guidelines do not include many specificities in marine communities. Thus many particular environments, such as coral reefs and isolated insular rocky shores, are poorly represented, and in many cases, only a fraction of their organic-life area comes under consideration (Leite, 2014).

São Paulo State was one of the first to create specific coastal management legislation. About 99,2% of the MPAs, created in 2008, are of multiple, sustainable use. The marine areas of full protection in the state are

relatively small and disconnected, what compromises ecological processes and the genetic and functional connectivity of target species (Leite, 2014).

The Ecological Station of Tupinambás, in which this study was undertaken, is at the highest level of protection. Founded in 1987, it is one of the first full protection marine conservation units in the region. Part of the area belongs to the Brazilian Navy, which, since 1979, has forbidden local fishing, anchorage and navigation, thereby diminishing anthropic pressure (Leite, 2014). Even so, illicit fishing has been frequently recorded (Gibran & Moura, 2012).

However, simply forbidding fishing may be insufficient to generate effective protection. Other features also contribute towards MPA efficacy, such as size, age, isolation, and well-enforced management (Edgar *et al.*, 2014). Therefore, long-term experimental investigation with the appropriate replication is required to better understand the processes underlying recovery, as well as to assess the effects arising from MPA protection (Bevilacqua *et al.*, 2006).

When considering that the main goal of monitoring programs is to detect temporal changes in communities, it is crucial that spatial scales generating significant variation data are incorporated and sufficiently represented by an adequate number of replicates. On failing to do so, the changes observed over time may be mistaken for natural spatial variation within the habitat under investigation (Coleman, 2002). Even when assessing reserve effects, one must take seascape variability under consideration, so that protection effects are not confused through habitat heterogeneity (Huntington *et al.*, 2010).

Conservation initiatives must thus incorporate knowledge on the appropriate scales of spatial variation of their targets. Hierarchical analysis of this variation should also involve the investigation of assemblage distribution, so as to fully represent the complexity of the natural system

under study (Benedetti-Cecchi, 2001). Since ecological patterns and the sustaining laws, rules and mechanisms depend on the organisms involved and their environment (Lawton, 1999), the spatial distribution and biodiversity scale of a particular location (e.g., a conservation unit) need to be enlightened. By doing so, the processes that maintain these patterns can be inferred. These, by definition, are the ones that need to be protected. At the point where they operate within different spatial scales and begin to fail near range extremities (Underwood, 1997, Soulé, 1985), efforts should be channeled towards ensuring their conservation, thereby guaranteeing long-term biodiversity persistence (Lourie & Vincent, 2004; Bertocci *et al.*, 2012).

Characterization of Benthic Communities

Gaps in the data used for modeling human impacts, further emphasize the need for basic research, such as habitat-type distribution (Halpern *et al.*, 2008). Moreover, methods for evaluating marine habitat sensitivity to human impacts are urgently required, in order to develop the appropriate management plans (Fraschetti *et al.*, 2008). Most studies on the impacts of climate change on the biota are more often focused on the individual level, with only a few dealing with communities as a whole, or higher levels of organization (Harley *et al.*, 2006). According to Fraschetti *et al.* (2008), habitat-level evaluation still faces many obstacles worldwide. There is a shared ambiguous classification, due to the lack of a common vocabulary, as well as a single, comprehensive system of identification and classification. In addition, there are difficulties in collecting high-resolution data concerning habitat extension and organism distribution.

A good investigation method consists of an efficient tradeoff between results accuracy and sampling cost, as regards time and funds. Some techniques provide an appreciable differential in the advance of

marine community research. Random sampling and the use of transects allowed the extrapolation of data to a larger area (Ribeiro, 2010), on the condition that enough replicas are placed. These still common approaches enable time saving qualitative description and pattern observation, through eliminating the need for sampling an entire area (Ribeiro, 2010).

Non-invasive methods, such as Direct Field Observations, are preferable to destructive sampling (Godet *et al.*, 2009). Imaging techniques, such as photographs and video-transects, are powerful tools for investigating marine communities. Results obtained by these methods, similar to those from conventional ones, are obtained in a much reduced time (Pech, 2004; Pereira Filho, 2008). In spite of its still limited use, photo-quadrats facilitate efficient and cost-effective quantitative estimation of benthic communities (Van Rein *et al.*, 2011). Over the past fifty years, and thanks to these methods, a great jump was taken towards the understanding of benthic communities, animal behavior and ecosystem structure (Solan *et al.*, 2003; Pech *et al.*, 2004). The development of digital equipment and computer image processing, from the 90's on, has been of even greater help in advancing analysis techniques (Pereira Filho, 2008).

Imaging techniques allows time saving in the field by leaving organism identification to the laboratory. Nonetheless, such identification at the species level is often impossible or extremely difficult. Very often, essential parts are missing, there is the need for special techniques, or experts, the latter many times unavailable (Pereira Filho *et al.*, 2008). Furthermore, in many cases image processing does not allow for the implementation of such fine taxonomic resolution. Thus, new operational units, other than species, have been created and are being used nowadays (Berchez *et al.*, 2005), thereby facilitating the investigation of larger areas in less time.

In the 90's, Brazilian researchers started using the concept of functional groups (Ribeiro, 2010). While presence of species varies, in the same community, a functional group remains relatively stable in time and space, thereby facilitating the observation of patterns (Steneck & Dethier, 1994). Concepts of functional groups and taxonomic resolution were proposed, based on morphological and ecological attributes (Veiga *et al.*, 2013). These have been tested by researchers as species surrogates to detect adequate representation of patterns of spatial variability on multiple scales, which would reduce thus the time and resources necessary for taxa identification (Smale, 2010).

Veiga *et al.* (2013) showed consistent patterns, when using functional groups and species in algal assemblages in temperate environments. Apart from a certain loss of information on wider scales, due to the increase in rare species, they confirmed that functional groups may be used as surrogates for monitoring studies and assessing spatial variability in such communities. In other studies, and when using wider taxonomic resolution, it was found that in aggregations up to the family level, there was no alteration in the spatial patterns of assemblage structure. Furthermore, it was considered the most appropriate resolution for effective cost monitoring and ecological research for both algal (Smale *et al.*, 2010) and invertebrate (Anderson *et al.*, 2005) assemblages.

The field of landscape ecology began to be applied in Brazil at the start of this century. In its main approaches, the geographical and the ecological, the landscape is considered as a heterogeneous spatial entity (Metzger, 2001), the seascape likewise. Rocky shores, by presenting vast spatial heterogeneity, comprise a multifaceted mosaic with many characteristic habitats, thereby representing a good model for testing this method on smaller scale (Ghilardi *et al.*, 2008). Depending on the study aims, the scale and biological level of the landscape within the spatial

heterogeneity are determined by the observer. However, in landscape ecology this is usually applied to very large areas (Metzger, 2001).

Statistical analysis, mainly multivariate, was introduced into Brazil in the 80's as a synthetic describer of marine community distribution, with the aim of encountering natural patterns in organism distribution. This approach, which facilitates the observation of phenomena normally invisible from rough data, has inaugurated a new group of researchers in Brazil (Ribeiro, 2010). According to the macroecological approach, ecological systems are not simply casual collections of organisms interacting at random, but present a great deal of order in the form of the structure and dynamics of the system as a whole, and of the organisms themselves, as well as the nature of their mutual interactions within their environment. This order has possibly been better revealed in certain statistical patterns (Brown, 1999).

The description of spatial or temporal variability patterns requires complex analysis. Nested sampling designs associated with variance analysis have proven to be powerful tools for investigating these patterns across a hierarchy of scales (Benedetti-Cecchi, 2001; Fraschetti *et al.*, 2005; Martins *et al.*, 2008). Nonetheless, this method is not free of flaws. Sampling intensity, therefore statistical power, increases lower in the hierarchy, thereby preventing a direct comparison of the variability magnitude across scales (Fraschetti *et al.*, 2005). To overcome this, actual variances can be estimated to guarantee independence and allow comparison (Benedetti Cecchi, 2001; Fraschetti *et al.*, 2005; Martins *et al.*, 2008). This approach can be applied to a wide range of ecological studies, dealing with island ecology, by clarifying issues on intrinsic variability in oceanic islands (Martins *et al.*, 2008).

In the 60's, MacArthur & Wilson (1963) published the Equilibrium Theory of Island Biogeography. This is essentially stochastic and

postulates that assemblage turnover is a result of the balance between extinction and immigration (Whittaker, 2000; Martins *et al.*, 2008). For a time, it remained paradigmatic, until such time as further observations lead to the development of other complementary theoretical frameworks to better explain the complexity of insular environments (Whittaker, 2000). Other theories are constantly being developed, such as those regarding metapopulations and static equilibrium (Whittaker, 2000; Martins *et al.*, 2008). In the latter, habitat is a determinant factor for assemblages, instead of being the result of purely stochastic variation (Whittaker, 2000).

The importance of including spatial and temporal scales when analyzing species-area relationships in insular communities has already been commented on. The significance of factors, such as area, isolation and habitat diversity, depends on their local variation. Once scale is considered as an organizing principle, there should be enlightenment on many of the contradictory conclusions about island theories (Whittaker, 2000).

Present study

By combining imaging techniques with the consideration of dominant species and feasible biological units, it is possible to rapidly assess insular benthic communities and analyze their general appearance and spatial distribution patterns. As hierarchical analysis of variance facilitates the investigation of these patterns within a range of spatial scales, this could be useful as a baseline for further research and management.

The aim was to evaluate the distribution patterns of the rocky shore subtidal benthic community of 3 islands in the MPA “Ecological Station of Tupinambás” (Ecoregion 180 – Southeastern Brazil, Spalding *et al.*, 2007), as a way of determining the most significant assemblage variation at two depth intervals among four different spatial scales, ranging from

centimeters to tens of kilometers. The idea was to arrive at a better understanding of the most important processes influencing this system, as well as to provide subsidies for monitoring implementation.

Since no other work has yet been done within a range of spatial scales in the region, it was not clear what to expect in advance, as regards pattern variation, especially since patterns are unique for each system (Fraschetti *et al.*, 2005). Hence, work was limited to testing the null hypothesis that spatial patterns are invariant among and across scales. However, as studies about scales of variation in insular marine environments have already been carried out in other regions, this led to the hypothesis that spatial variability would be found to be high on the larger spatial scale (differences between islands), due to the importance of regional-scale processes influencing such assemblages (Martins *et al.*, 2008). Furthermore, many descriptive studies have been undertaken in SE Brazil, thereby providing clues about what kind of community could be expected. This region was found to have been structured by macroalgae, in particular *Sargassum* spp., as well as Articulated Calcareous Algae (Eston *et al.*, 1986, Figueiredo *et al.*, 1994, Széchy & Paula, 2000, Amado Filho *et al.*, 2006, Ghilardi, 2007), so these were expected to be found in abundance.

Methodology

Study location

The present study took place in the Ecological Station of Tupinambás, a Complete Protection Unit since 1987. Thereby, with the exception of research, no other activity can be performed within its range (Leite, 2014). The ES encompasses part of the Alcatrazes Archipelago, as

well as the Cabras and Palmas Islands, in addition to the marine portion on the 1 km radius from all formations. They are on the São Paulo State continental shelf, between 23° and 24°S and 44° and 45°W. Some components of the archipelago, as well as the Alcatrazes Island, are not part of the ES of Tupinambás. Nonetheless, these and the coastal area of the country belong to the MPA “Alcatrazes de São Sebastião”. The Brazilian Navy, in 1979, established a training area in the archipelago, further prohibiting fishing and anchoring in the remaining areas, other than those of the ES. Therefore, this area became of full protection (Leite, 2014). The Archipelago comprises five islands, four islets, five flagstones and two shoals, located 35 Km from the coast (Rocha & Bonnet, 2009). Cabras and Palmas Islands are near Anchieta Island, 9 Km from the coast. Sampling was undertaken at the Islands of Oratório, Sapata and Palmas (Fig 1).

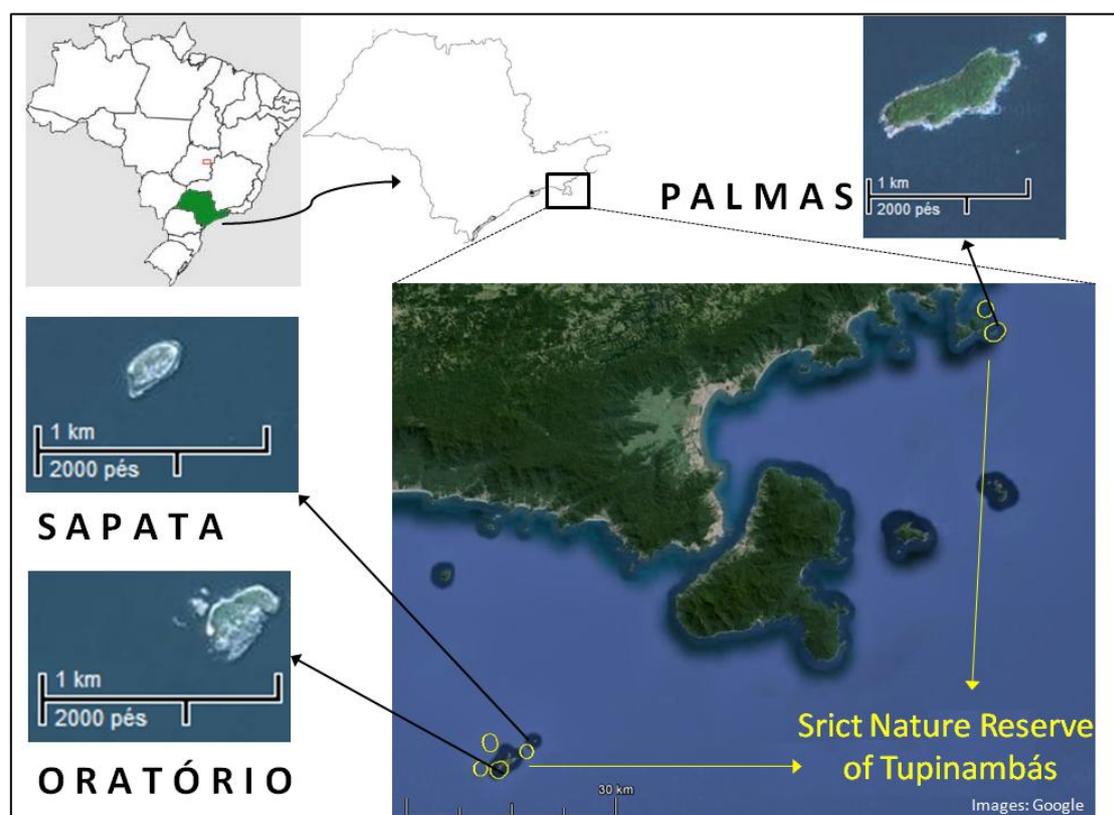


Fig. 1 Study area with Strict Nature Reserve of Tupinambás' boundaries and islands of sampling.

At the archipelago, the water column physical properties are homogeneous in the winter. However, in the summer, it has an accentuated thermocline. It is surrounded by sandy bottoms, and subject to direct incidence of S and SW waves, which eventually inverse (Leite, 2014). The region is under influence of Tropical Waters, the Brazil Current and the Central Waters of the South Atlantic (Leite, 2014).

Sampling design

Sampling followed a nested design (Fig. 2) and was undertaken in the Southeastern Brazil Ecoregion (Spalding *et al.*, 2007) at the summer and winter of 2013 and summer of 2014. Three islands, separated by tens of kilometers, were randomly selected from a group of comparable islands, which possesses at least 300 meters of wave-protected coast (Fig. 1). On each island, two 100 meter length sectors, separated by hundreds of meters, were randomly selected along the wave-protected shore. On each sector, two 10 meter length sites, separated by tens, of meters, were randomly selected. To ensure all the sites were comparable, only slopes were sampled. If the drawn site was in boulders, the nearest slope was sampled and the coordinates recorded. On each site, two 2.5 meter length areas were sampled with four random samplings elements each. These were 50 x 50 cm photo-quadrats, and all 8 all them (4 from each area) were randomly assigned to 2 different groups. These groups of quadrats represented the levels of the smallest spatial scale: meters. Each area was sampled at two depth intervals: the shallower subtidal, from 1 to 5 meters depth, comprising also the sublittoral fringe; and the lower subtidal, from 5 to 10 meters depth.

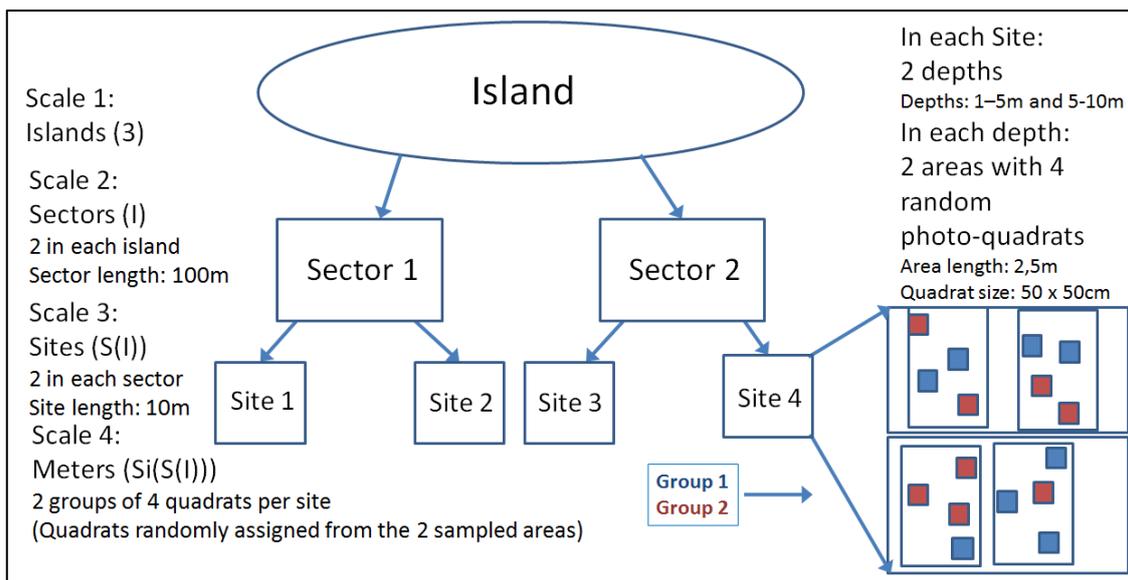


Fig. 2 Nested design and factors. The scheme represents how sampling was performed in each one of the three islands. All factors were random.

Sampling methods

The position of sampling units was previously determined by hypothetically dividing the study area into quadrats the same size as the sampling element. This created an imaginary grid in the coast in which the sampling units were randomly placed. Their coordinates were thus taken so their position could be located in the field with the aid of a diving computer (Subgear, model XP10) and a marked cable (Fig. 3). The “random numbers” feature, from the Microsoft Excel software was utilized to randomize the sampling elements.

In addition, destructive samples of algae and sessile invertebrates were collected with the aid of a spatula and draining bags, and further fixed in formaldehyde 4% mixed with seawater to aid the identification of taxa in the laboratory (Fig. 3). The inclination of the substratum was measured for each sampling element with an inclinometer (Fig. 3). Photographs were taken from a digital camera, (Canon PowerShot, model G12 – 10 Mega Pixels) in a waterproof case attached to a supporter (Fig. 3).

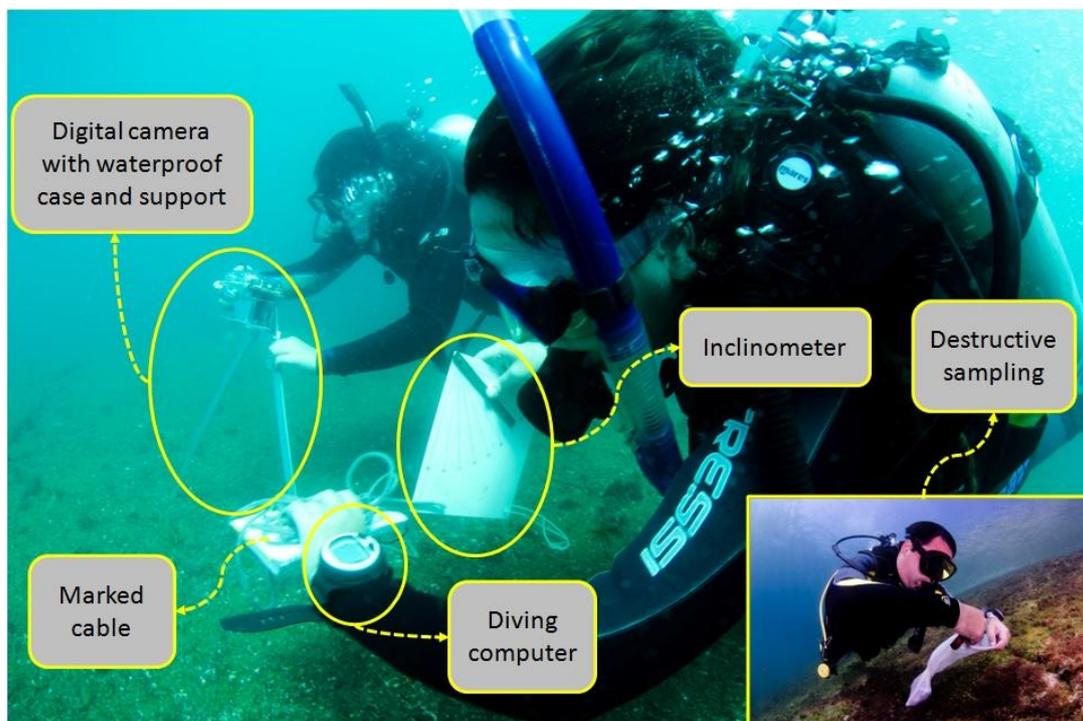


Fig. 3 Data collection in the field and sampling equipments (Photographs: Leo Francini).

Data analysis

The primary descriptor of the community for the quantitative analyses was the biological units' percent cover. These were species, morphological groups or taxonomic levels higher than species. They were designated according to the possibility of identification from the photographs and samples. Biological units are commonly used by researchers to overcome identification challenges, as pointed out by Murray *et al.* (2002). Dominant organisms were identified to species level, when possible. When field collection of a given organism was not possible (such as in the case of Encrusting Coralline Algae) or species were undistinguishable from each other in the photographs (as in the case of Articulated Calcareous Algae), they were analyzed as morphological groups. When the collected sample did not allow identification into species level, it was considered as the next higher taxonomic category possible. Rare and less abundant species were not identified.

The images were treated on the Adobe Photoshop software before the analysis (Fig. 4). After the treatment, the images were converted to the JPEG format and analyzed in the PhotoQuad software, in order to obtain the cover data from the photo-quadrats (Trygonis & Sini, 2012). This software plots random points in the image, which were identified as the name of the species or morphological group beneath it (Fig. 5). Fifty points were scattered in each photo-quadrat. According to other studies which utilized this method, this number was considered sufficient (Pereira Filho, 2008; Martins *et al.*, 2008; Ribeiro, 2010). The percentage cover was thus converted by the software into Microsoft Excels' tables.

Secondary cover was only considered in the cases when an association of two equally represented species was in the given patch. Therefore, the analyzed assemblages are multilayered. For instance, when in a given patch of turf algae, the epiphytes were abundant so the primary cover was almost not visualized, or when turf algae completely covered mussels or barnacles, these were considered as an association. In these cases, each layer was considered a variable and both had the same value. If the same biological unit appeared both as primary and as secondary cover, it was discriminated and considered as two different variables.



Fig. 4 Same photo-quadrat before Photoshop treatment (left) and after treatment (right).
(Photograph: Leandro Santos).

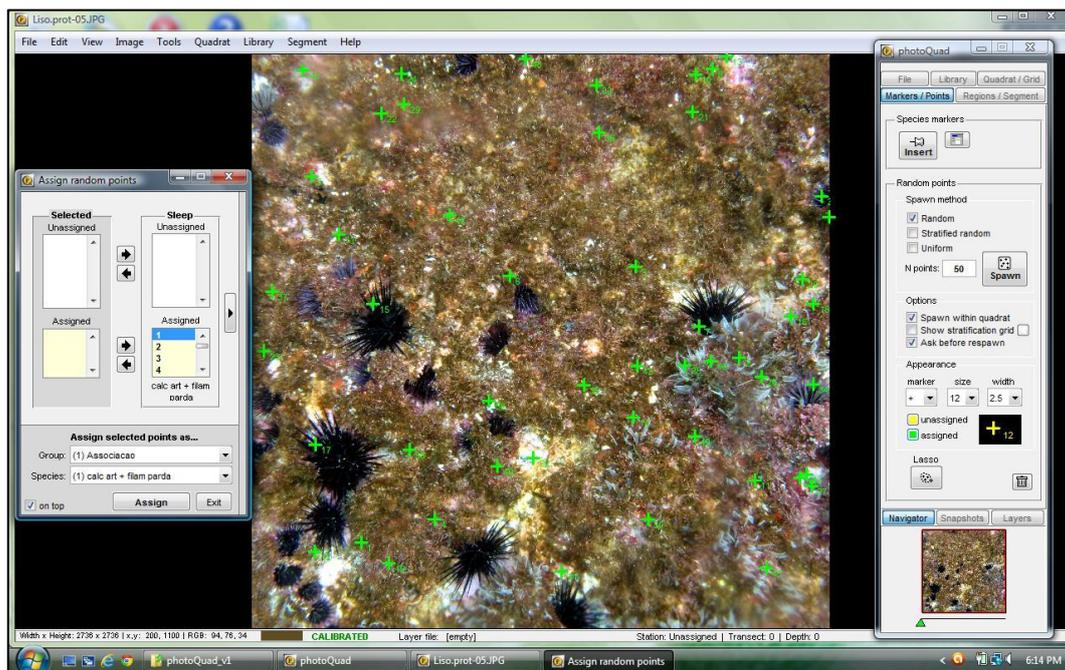


Fig. 5 PhotoQuad software showing a 50 x 50cm photo-quadrat with random points scattered.

Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) was performed to examine spatial variation in the whole assemblage, based on Bray-Curtis dissimilarities. The inclination of the substrate was analyzed as a covariant. Factors were Island (3 levels; random), Sector (2 levels; random, nested in islands), Site (2 levels; random, nested in sectors and islands) and Meters (2 levels; random, nested in sectors, sites and islands).

Spatial patterns from the cover of dominant species and morphological groups were analyzed individually by hierarchical analysis of variance, based in Euclidean distances (Underwood & Chapman, 1996). Cochran's C-test was performed *a priori* to assess variance homogeneity. When the null hypothesis was rejected, therefore variances were heterogeneous, a stricter criterion of p (< 0.01) was undertaken (Underwood, 1997).

Both uni and multivariate analyses were performed in the software PERMANOVA6 (Anderson, 2001). All analyses were performed on

untransformed data using 999 permutations. Monte Carlo p -values were considered in all cases. Pairwise comparisons were performed *a posteriori*, when suited, using 999 random permutations. Variance components were calculated in order to assess the variation associated with each scale. These calculations were undertaken from MS estimates by dividing the difference between the MS of the term of interest and the MS of the term hierarchically below by the product of the levels of all terms below (Martins *et al.*, 2008). Negative values were set to zero according to Fletcher & Underwood (2002).

Non-metric multidimensional scaling ordinations (nMDS; Kruskal & Wish, 1978) were performed from abundance data of the whole assemblage. Ordinations were obtained from the sites' centroids based on Euclidean distances (Underwood & Chapman, 1998), in the software PRIMER 6 (Clarke & Gorley, 2006).

Principal components analysis (PCA) was undertaken in order to detect the most important species structuring the assemblage. Ordinations were based on Bray-Curtis dissimilarities in the software PRIMER 6.

Results

The encountered species and morphological groups, as they were identified in the photographs, are represented in Table 1, along with the codes of those represented in the Principal Components Analysis. The dominant species and biological units are highlighted.

Among the most abundant, the Rhodophyta were represented by the group "Articulated Calcareous Algae" (ACA), mainly constituted by *Amphiroa fragilissima* and *Amphiroa beauvoisii*, but also including *Jania* sp. They exhibited a great amount of epiphytes, which were mostly red filamentous algae and, in the summer of 2014, almost exclusively the

filamentous phase of *Asparagopsis taxiformis*. Other dominant Rhodophyta were the cylindrical alternant phase of *Asparagopsis taxiformis*, and the morphological group of “Encrusting Coralline Algae”. Other common organisms were the Phaeophyta *Sargassum* sp. and *Lobophora variegata*, the Chlorophyta *Codium intertextum*, the Crustacea *Megabalanus* sp., the Echinodermata *Echinometra lucunter*, the Porifera *Tedania ignis*, the Bivalvia *Perna perna* and the Tunicata *Didemnum perlucidum*.

Several other organisms were present in the assemblages, but due to their low abundance, were not always identified to species level. Among them, the most noticeable were other macroalgae, such as the Phaeophyta *Dictyota* sp., *Canistrocarpus cervicornis* and *Padina gymnospora*, the Rhodophyta *Wrangelia argus* and other red filamentous algae, the Chlorophyta defined as green filamentous algae, several encrusting sponges and ascideas, encrusting bryozoans, including *Schizoporella errata*, hydroids, the starfish *Echinaster brasiliensis* and the anthozoans *Mussismilia hispida*, *Bunodosoma caissarum*, *Carijoa riisei*, *Parazoanthus* sp. and *Leptogorgia punicea*, the latter always in association with the ophiuroid *Ophiothela mirabilis*.

Considering species, morphological groups and organisms collapsed into higher taxonomic groups, the total of 29 biological units was found. In the shallower assemblage, the total number of biological units found in the summer of 2013 was 24, in the winter, 29 and 22 in the summer of 2014. In the lower assemblage, there was 20 in the summer of 2013, 26 in the winter and 25 in the summer of 2014.

Table 1 Biological units, as they were identified from the photographs, found at all sites and periods of sampling. The dominant are marked with an “*”. Codes used in the Principal Component Analysis are represented in the column at the right of each biological unit.

Phylum	Family	Biological Unit	Code	Phylum	Class	Biological Unit	Code			
Rhodophyta	Corallinaceae	Articulated Calcareous Algae	CAR	Arthropoda	Cirripedia (Infraclass)	<i>Megabalanus</i> sp. *	MEG			
		Encrusting Coralline Algae *	CCR			Echinodermata	Echinoidea	<i>Echinometra lucunter</i>	ECH	
	Bonnemaisoniaceae	<i>Asparagopsis taxiformis</i> *	ASP					Asteroidea	<i>Echinaster brasiliensis</i>	-
	Wrangeliaceae	<i>Wrangelia argus</i>	-						Ophiuroidea	<i>Ophiothela mirabilis</i>
Unknown	Red Filamentous Algae	-	Porifera	Demospongiae	<i>Tedania ignis</i> *	TED				
Phaeophyta	Sargassaceae	<i>Sargassum</i> sp. *			SAR	Mollusca	Bivalvia	<i>Perna perna</i>	PER	
		Dictyotaceae	<i>Lobophora variegata</i>	LOB	Chordata			Ascidiaaceae	<i>Didemnum perlucidum</i>	DID
			<i>Dictyota</i> sp.	-		Encrusting ascideas	-			
			<i>Padina gymnospora</i>	-						
<i>Canistrocarpus cervicornis</i>	-									
Chlorophyta	Codiaceae	<i>Codium intertextum</i> *	COD	Bryozoa	Gymnolaemata	<i>Schizoporella errata</i>	-			
		Unknown	Green Filamentous Algae			-	Unknown	Encrusting Briozoans	-	
				Cnidaria	Hydrozoa	Hydroids	-			
						Anthozoa	<i>Mussismilia hispida</i>	-		
							<i>Bunodosoma caissarum</i>	-		
							<i>Carijoa riisei</i>	-		
							<i>Parazoanthus</i> sp.	-		
				<i>Leptogorgia punicea</i>	-					

The shallower assemblage was mostly dominated by Articulated Calcareous Algae (ACA) in all periods. This assemblage was represented by more dominant taxa in the winter than in both summers. In the summer of 2013, the other dominants, apart from ACA, were *Sargassum* sp., *Megabalanus* sp. and *Codium intertextum*. Figure 6A illustrates the mean cover of those dominant groups in each site for this period. Mean percentage cover varied among islands from 59.56% to 74.81% for Articulated Calcareous Algae, from 8.9% to 13.75% for *Sargassum* sp., from 2.81% to 6.31% for *Megabalanus* sp. and from 0.06% to 6.17% for *C. intertextum*.

In the winter of 2013, along with Articulated Calcareous Algae, were *Codium intertextum*, Encrusting Coralline Algae, *Asparagopsis taxiformis*, *Megabalanus* sp., *Tedania ignis* and *Sargassum* sp. The mean cover of those biological units in each site is illustrated in Figure 6B. Mean percentage cover among islands varied from 48.75% to 89.56% for Articulated Calcareous Algae, from 0% to 8.35% for *Codim intertextum*, from 0.38% to 9.17% for *Megabalanus* sp., from 0% to 5.31% for *Sargassum* sp., from 2.77% to 7% for Encrusting Coralline Algae, from 0% to 13.48% for *Asparagopsis taxiformis* and from 0.94% to 2.88% for *Tedania ignis*.

In the summer of 2014, the dominants were Articulated Calcareous Algae (ACA) and *Asparagopsis taxiformis*. Mean cover among islands varied from 59.43% to 87.19% for ACA and from 1.25% to 41.69% for *Asparagopsis taxiformis*, and their mean cover for each site is represented in Figure 10C. The lower assemblage was also dominated mostly by Articulated Calcareous Algae in all periods. Along with ACA, other dominants were *Sargassum* sp. and *Codium intertextum* in the summer of 2013; *Codium intertextum* in the winter; and *Codium intertextum* and *Asparagopsis taxiformis* in the summer of 2014.

The lower assemblage was also mostly dominated by Articulated Calcareous Algae (ACA) in all periods. Along with ACA, the other dominants were *Sargassum* sp. and *Codium intertextum* in the summer of 2013. Figure 7A illustrates the mean cover of those dominants in each site for this period. ACA had a mean percentage cover varying among islands from 55.88% to 78.38%, *Sargassum* sp., and *Codium intertextum*, varied among islands from 9.19% to 19.88% and from 0% to 27%, respectively.

In the winter of 2013, the other dominant was *Codium intertextum*. The mean cover of these biological units for each site is represented in Figure 7B and mean percentage cover among islands varied from 36% to 89% and from 0% to 52% for Articulated Calcareous Algae and *C. intertextum*, respectively.

The other dominants in the summer of 2014 were *Codium intertextum* and *Asparagopsis taxiformis*. Articulated Coralline Algae presented mean cover values that varied among islands from 46.69% to 86.31%, *Codium intertextum* varied from 0% to 34.81% and *Asparagopsis taxiformis* from 0% to 17% and the mean cover for each site is illustrated in Figure 7C.

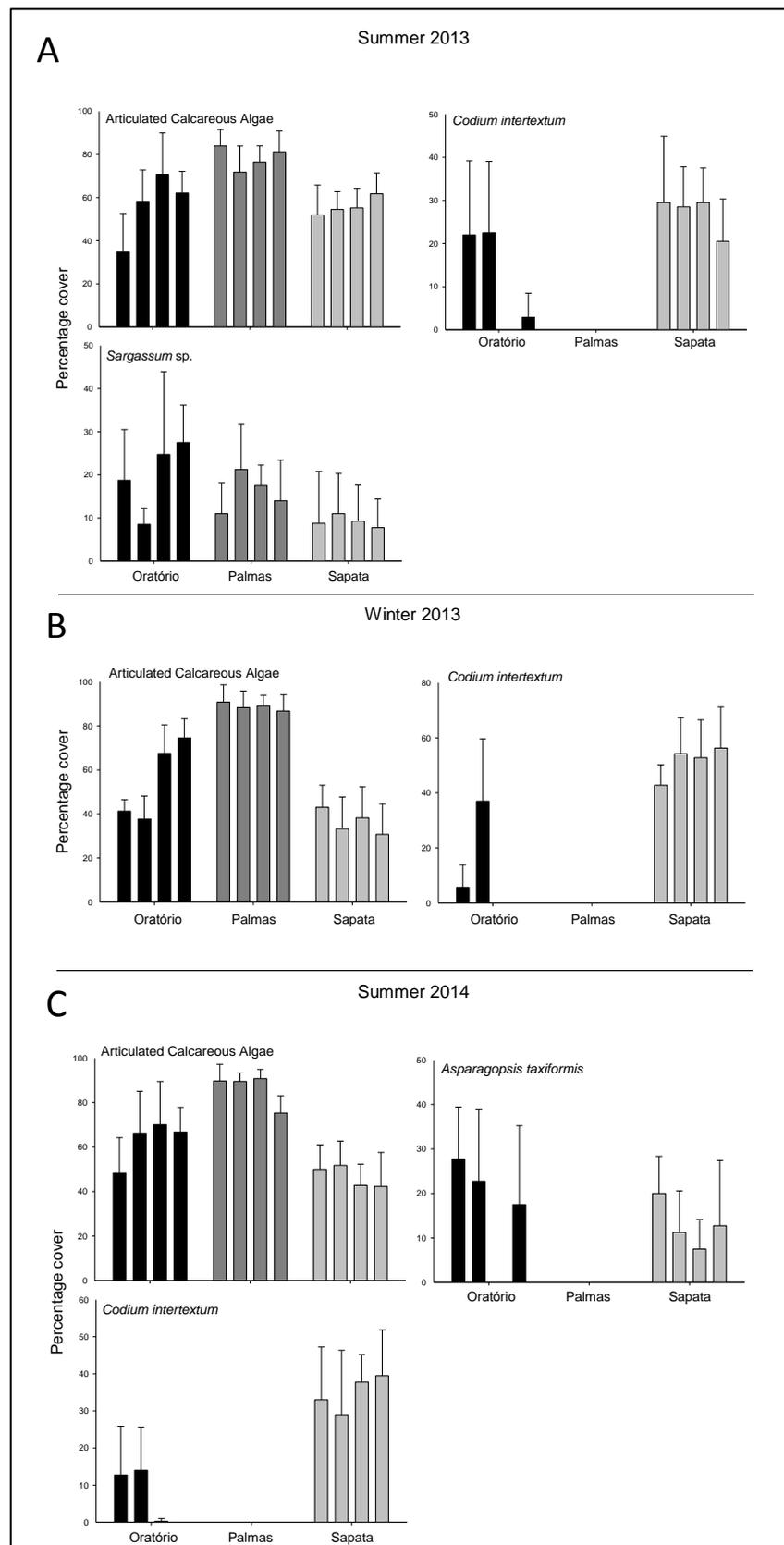


Fig. 7 Lower (5 – 10 m depth) assemblage's mean (\pm SE) cover of dominant taxa. Each bar represents one site on each island. (A) Data from the summer of 2013; (B) Data from the winter of 2013; (C) Data from the summer of 2014.

Multivariate Analyses

Shallower Interval (1 – 5 m depth)

Table 2 presents the results for spatial differences on all scales, revealed by PERMANOVA. There were 3 relevant scales of spatial variation, which varied according to sampling period: the scale of island in all sampled periods, the scale of sector in the summer of 2014 and the scale of site in the summer of 2013. No significant differences were found on the scale of meters. Estimates of multivariate variation were higher on the scale of island at all times, followed by the scale of sites in the summer of 2013, and by sector in the winter of 2013 and summer of 2014, when the difference from island and sector was the smaller. Residual variation, indicating multivariate heterogeneity among quadrats was much larger than variation on any other scale.

Pairwise comparisons performed *a posteriori* on the factor Island, are presented in Table 3. In the summer and winter of 2013, all three islands were significantly distinct one from another. In the summer of 2014, only the islands of Palmas and Sapata were significantly different from each other.

Visual inspection of the nMDS plots are illustrated in Figure 8 and reflected the results from the Pairwise comparisons (Table 3, Fig. 8). There was a clear separation of the islands in the summer and winter of 2013 (Fig. 8A and B), and in the last period (Fig. 8C), the assemblage from Oratório comprises similar sites as both of the other islands, which are very far from each other in the multivariate space.

Table 2 Results of PERMANOVAs testing for spatial differences in structure of assemblages in the shallower interval (1 – 5 m depth) at scales of Island, sector, site and meters. Analyses based on Bray-Curtis dissimilarities from untransformed data. Each term was tested using 999 random permutations of appropriate units. Inclination of the substrate was included as a covariant. Estimates of multivariate variation are given for each spatial scale. *P*-values of Monte Carlo were considered.
* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, ns: not significant.

Source	Df	1 – 5m Depth								
		Summer 2013			Winter 2013			Summer 2014		
	MS	<i>F</i>	Estimates of spatial variation	MS	<i>F</i>	Estimates of spatial variation	MS	<i>F</i>	Estimates of spatial variation	
Is	2	4142.86	6.68**	110.07	13680.416	9.40**	382.04	11729.29	4.60*	286.79
Se(Is)	3	620.58	0.68 ^{ns}	0.0	1455.22	1.80 ^{ns}	40.32	2551.98	3.93***	118.96
Si(IsxSe)	6	918.34	2.71***	72.51	810.14	1.39 ^{ns}	28.19	648.63	1.56 ^{ns}	29.02
Me(IsxSexSi)	12	338.25	0.70 ^{ns}	0.0	584.65	1.03 ^{ns}	3.70	416.48	0.91 ^{ns}	0.0
Residual	71	482.62		482.62	569.86		569.86	458.58		458.58
Total	95									
Transformation		None			None			None		

Table 3 Pairwise comparisons of the factor Island in the shallower assemblage (1 – 5 m depth). Tests performed using 999 random permutations. *P*-values of Monte Carlo were considered.
* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, ns: not significant.

Groups	1 – 5m depth		
	Summer 2013	Winter 2013	Summer 2014
	<i>t</i>	<i>t</i>	<i>t</i>
Oratório x Palmas	2.14*	3.88**	1.47 ^{ns}
Oratório x Sapata	2.02*	2.25**	1.21 ^{ns}
Palmas x Sapata	3.34**	3.94**	4.65**

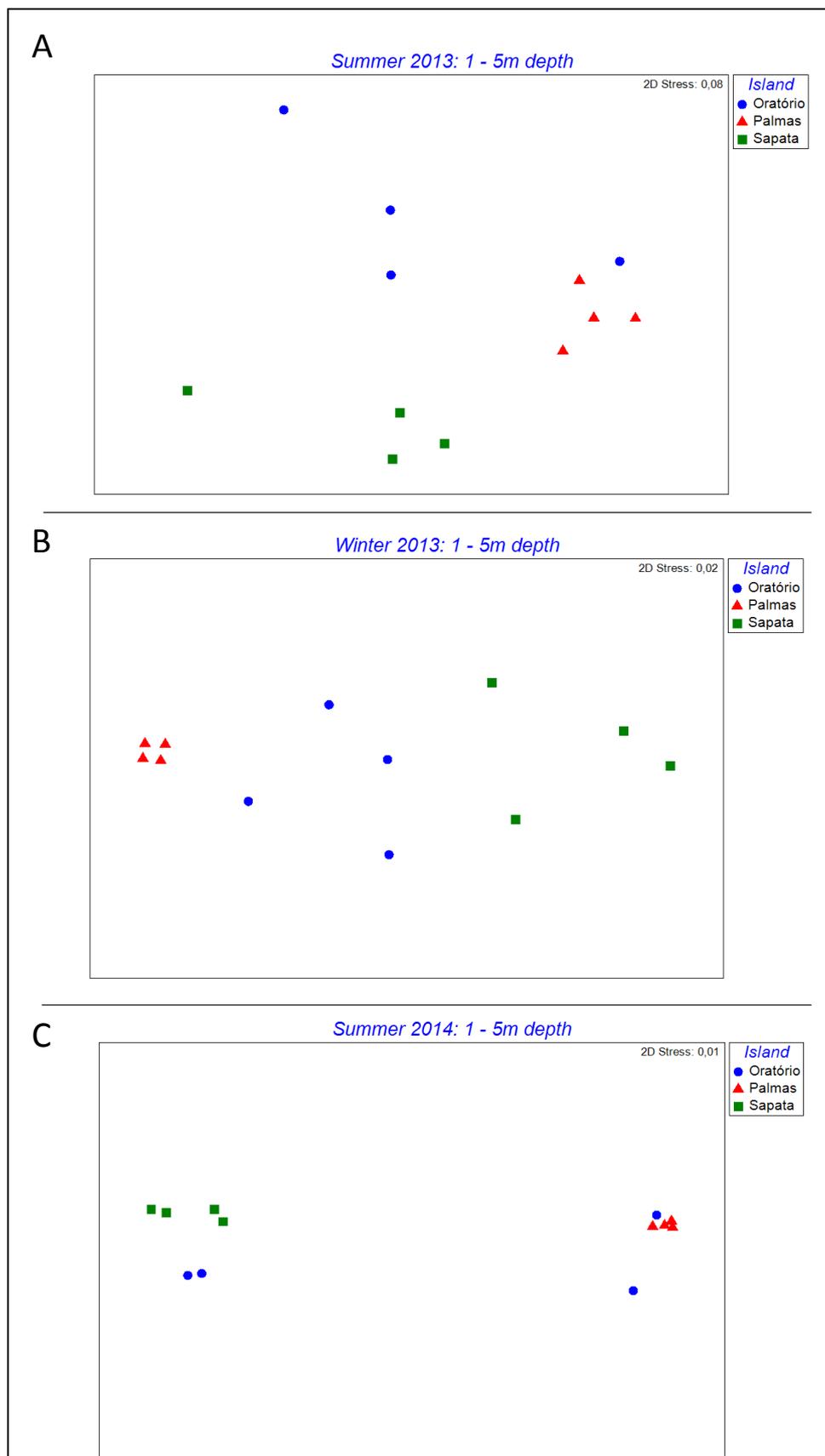


Fig. 8 nMDS ordinations from the shallower assemblage (1 – 5 m depth), representing the community structure of the (A) summer of 2013, (B) winter of 2013, and (C) summer of 2014. Each symbol represents the centroid for that site. Blue: Island of Oratório; Red: Island of Palmas; Green: Island of Sapata. Ordinations based in Euclidean distances.

As variation among sectors was significant in the summer of 2014, Pairwise comparisons were undertaken and revealed significant differences among the levels of the islands of Oratório ($t = 2.51$; $p = 0.015$) and Palmas ($t = 2.33$; $p = 0.033$), but not among the sectors of Sapata ($t = 0.67$; $p = 0.791$). For the scale of Site, with significant variation in the summer of 2013, only 1 of the 6 comparisons, among two sites of the island of Oratório, showed significant variation.

Figure 9 represents the Principal Components Analysis, which illustrates the biological units that most contribute to the samples' similarity in the multivariate space, as vectors. The species and morphological groups that best explained the assemblage's structure were the Articulated Calcareous Algae in all periods, together with *Sargassum* sp. in the summer of 2013 (Fig. 9A), *Codium intertextum* and *Asparagopsis taxiformis* in the winter (Fig. 9B) and *Sargassum* sp. and *A. taxiformis* in the summer of 2014 (Fig. 9C). On determining each island's structure, Articulated Calcareous Algae was the most important taxa for the Island of Palmas in all periods. The Island of Sapata varied between sampling periods. This island was structured mainly by *A. taxiformis* in the two last periods (Fig. 9B and C) and by *Megabalanus* sp., *Codium intertextum*, *Perna perna* and urchins altogether in the first summer (Fig. 9A).

The sites representing the Island of Oratório were more heterogeneous (Fig. 8) and showed no taxa strongly structuring this assemblage in the summer of 2013 (Fig. 9A). In the following summer Articulated Calcareous Algae and *A. taxiformis* (in its filamentous phase, as an epiphyte of Articulated Calcareous Algae) slightly structured this assemblage (Fig 9C), and in the winter, this island was structured mainly by Articulated Calcareous Algae and *C. intertextum* (Fig. 9B).

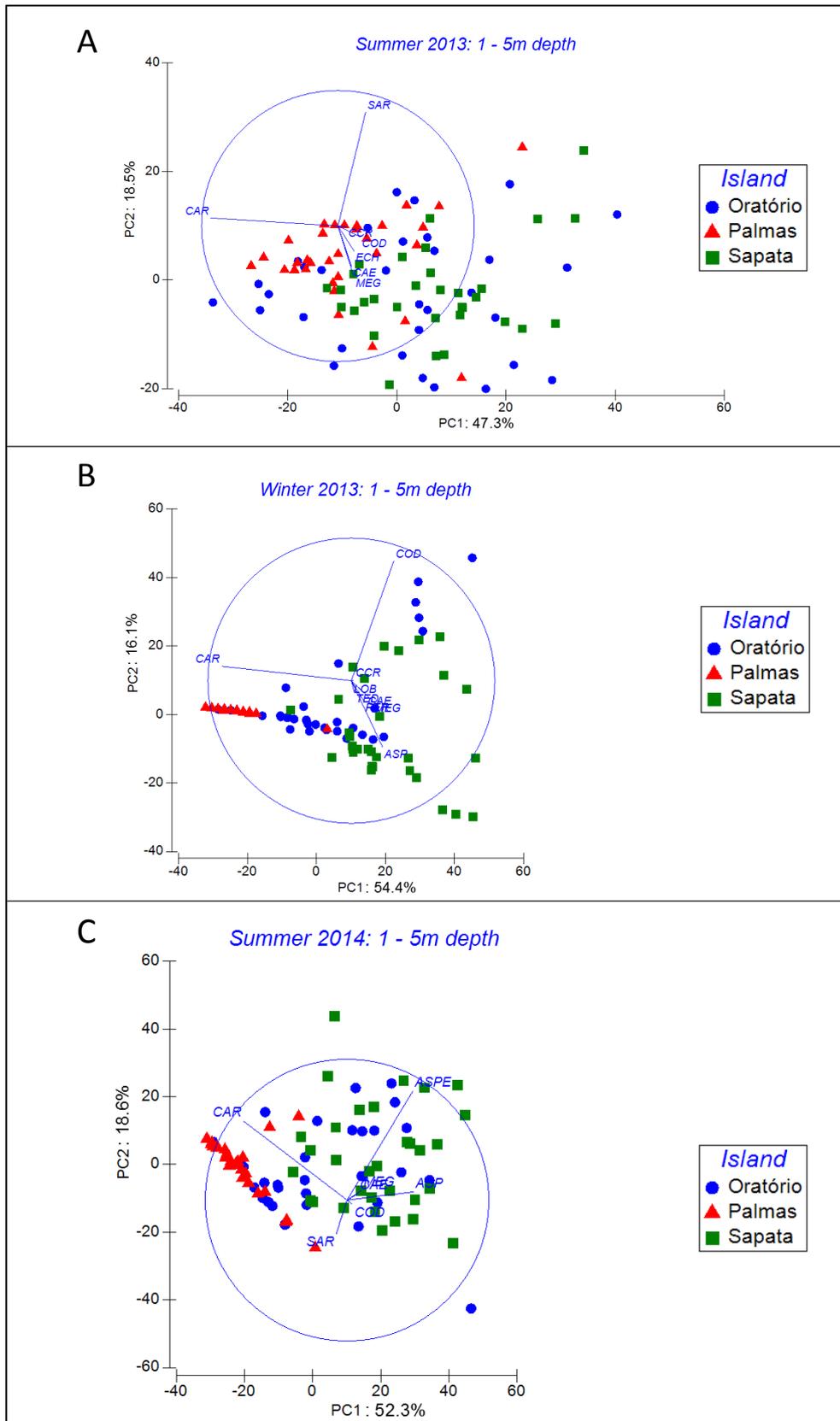


Fig. 9 Principal components analysis of the dominant taxa of the shallower assemblage (1 – 5 m depth), from (A) summer of 2013, (B) winter of 2013, and (C) summer of 2014. Blue: Island of Oratório; Red: Island of Palmas; Green: Island of Sapata. CAR: Articulated Calcareous Algae; SAR: *Sargassum* sp.; COD: *Codium intertextum*; ASP: *Asparagopsis taxiformis*; MEG: *Megabalanus* sp.; ECH: *Echinometra lucunter*; PER: *Perna perna*. ASPE: *Asparagopsis taxiformis* as epiphyte; CAE: Articulated Calcareous Algae as epiphyte. Ordinations based in Bray-Curtis dissimilarities.

Lower Interval (5 – 10 m depth)

The results of PERMANOVA for spatial differences at all scales are presented in Table 4. Analysis revealed 3 relevant spatial variation scales: the scale of Island was not significant only in the summer of 2013. In this case however, the p value was marginally significant ($p = 0.067$), suggesting attention direction to the Pairwise comparisons. Variation on the scales of Sector and Site were significant at all times. No significant differences were found at the scale of meters. Estimates of multivariate variation increased with increasing spatial scale. In other words, the values relative to the scale of island were always much higher than any of the scales below. Residual variation was larger than variation on all the other scales, except in the winter of 2013 and summer of 2014, when it was lower than variation among islands.

Pairwise comparisons undertaken *a posteriori* on the factor Island are presented in Table 5. Apart from the PERMANOVA results, which revealed non-significance among island in the summer of 2013 (Table 4), the islands of Palmas and Sapata were significantly different in the first two sampling periods, and all three of them were significantly distinct in the summer of 2014.

These results can be visualized in the nMDS plots, represented in Figure 10. There was a clear separation of the islands of Palmas and Sapata in the first two sampling periods (Fig. 10A and B), when Oratório's sites presented similarity with both. In the summer of 2014 (Fig. 10C), all islands form distinct groups.

Table 4 Results of PERMANOVAs testing for spatial differences in structure of assemblages in the lower interval (5 – 10 m depth) at scales of Island, sector, site and meters. Analyses based on Bray-Curtis dissimilarities from untransformed data. Each term was tested using 999 random permutations of appropriate units. Inclination of the substrate was used as a covariant. Estimates of multivariate variation are given for each spatial scale. *P*-values of Monte Carlo were considered. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, ns: not significant.

Source	df	5 – 10m Depth								
		Summer 2013			Winter 2013			Summer 2014		
	MS	<i>F</i>	Estimates of spatial variation	MS	<i>F</i>	Estimates of spatial variation	MS	<i>F</i>	Estimates of spatial variation	
Is	2	9117.74	3.44 ^{ns}	202.17	32895.62	9.34 ^{**}	917.87	22508.28	10.81 ^{**}	638.34
Se(Is)	3	2648.37	3.59 [*]	119.39	3523.64	3.23 [*]	152.07	2081.27	2.72 [*]	82.17
Si(IsxSe)	6	738.12	3.07 ^{**}	62.19	1090.55	3.90 ^{***}	101.40	766.60	2.91 ^{***}	62.88
Me(IsxSexSi)	12	240.60	0.73 ^{ns}	0.0	279.37	0.99 ^{ns}	0.0	263.56	0.65 ^{ns}	0.0
Residual	71	330.26		330.26	281.66		281.66	402.66		402.66
Total	95									
Transformation		None			None			None		

Table 5 Pairwise comparisons of the factor Island in the lower assemblage (5 – 10 m depth). Tests performed using 999 random permutations. *P*-values of Monte Carlo were considered * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, ns: not significant.

Groups	5 – 10m depth		
	Summer 2013	Winter 2013	Summer 2014
	<i>T</i>	<i>t</i>	<i>t</i>
Oratório x Palmas	1.51 ^{ns}	1.64 ^{ns}	2.32 [*]
Oratório x Sapata	0.64 ^{ns}	2.10 ^{ns}	3.27 ^{**}
Palmas x Sapata	5.90 ^{**}	11.49 ^{***}	6.19 ^{**}

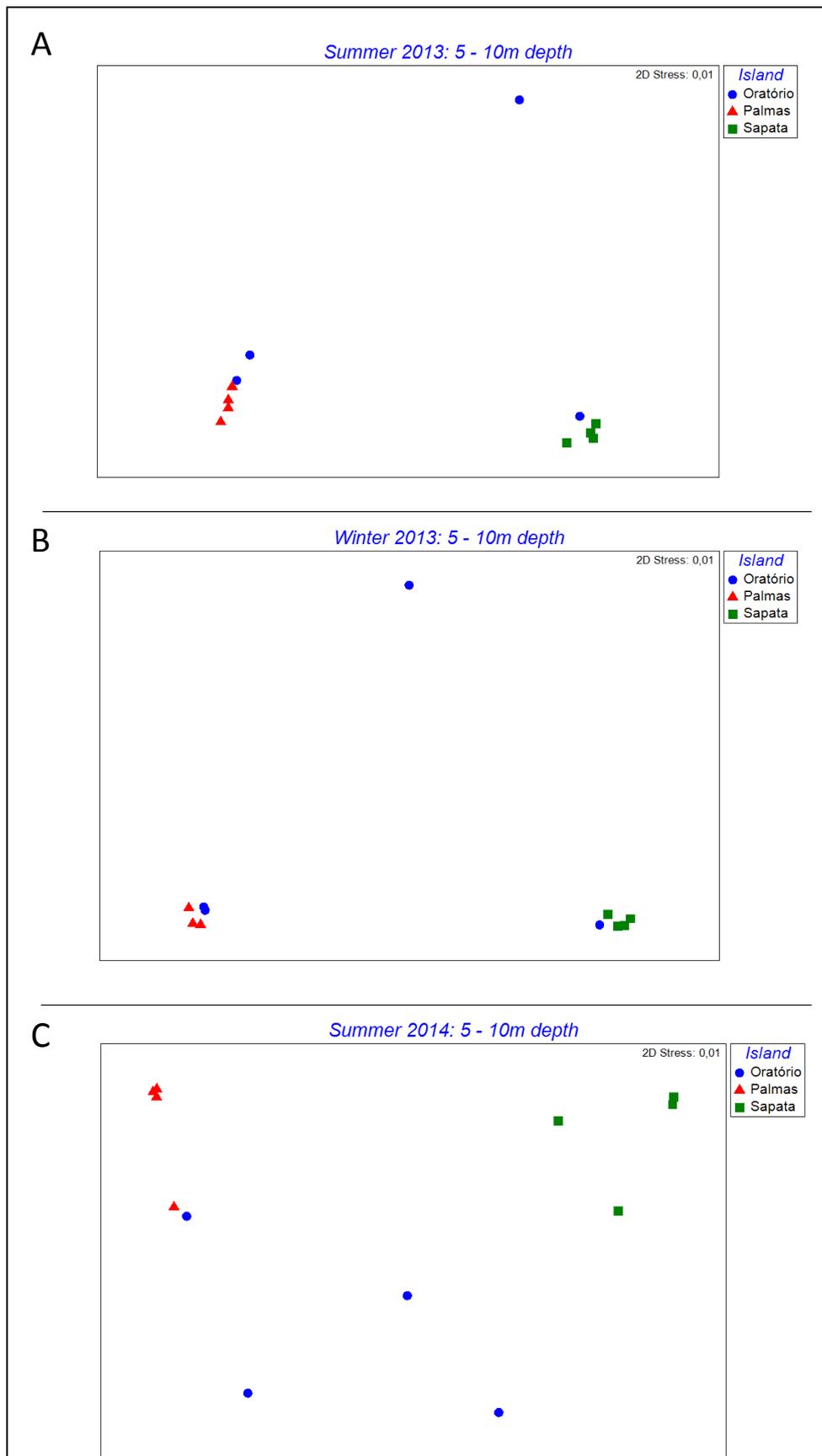


Fig. 10 nMDS ordinations from the lower assemblage (5 – 10 m depth), representing the community structure of the (A) summer of 2013, (B) winter of 2013, and (C) summer of 2014. Each symbol represents the centroid for that site. Blue: Island of Oratório; Red: Island of Palmas; Green: Island of Sapata. Ordinations based in Euclidean distances.

For the scale of Sector, pairwise comparisons did not reveal significant variation in any period. For the scale of Site, significant variation was found for 1 of 6 comparisons in the summer and winter of 2013, among sites of the islands of Palmas and Oratório, respectively. And 2 of 6 significant comparisons were found in the summer of 2014, among sites of the islands of Oratório and Palmas.

The biological units which most contributed to the similarity of samples were revealed by the Principal Components Analysis, illustrated in Figure 11. The ones best explaining the assemblage's structure were the Articulated Calcareous Algae and *Codium intertextum* for all periods, along with *Sargassum* sp. in the summer of 2013 (Fig. 11A), and *Sargassum* sp. and *Asparagopsis taxiformis* in the summer of 2014 (Fig. 11C).

The Island of Palmas was strongly structured by Articulated Calcareous Algae in all periods (Fig 11). Sapata was variable, but Articulated Calcareous Algae and *C. intertextum* slightly structured its assemblage in both summers (Fig. 11A and C), while in the winter, it was strongly structured by *C. intertextum* (Fig 11B). Oratório was very variable in both summers (Fig. 11A and C), but showed to be slightly structured by Articulated Calcareous Algae and *Sargassum* sp. in the latter (Fig. 11C), and strongly structured by Articulated Calcareous Algae in the winter (Fig. 11B).

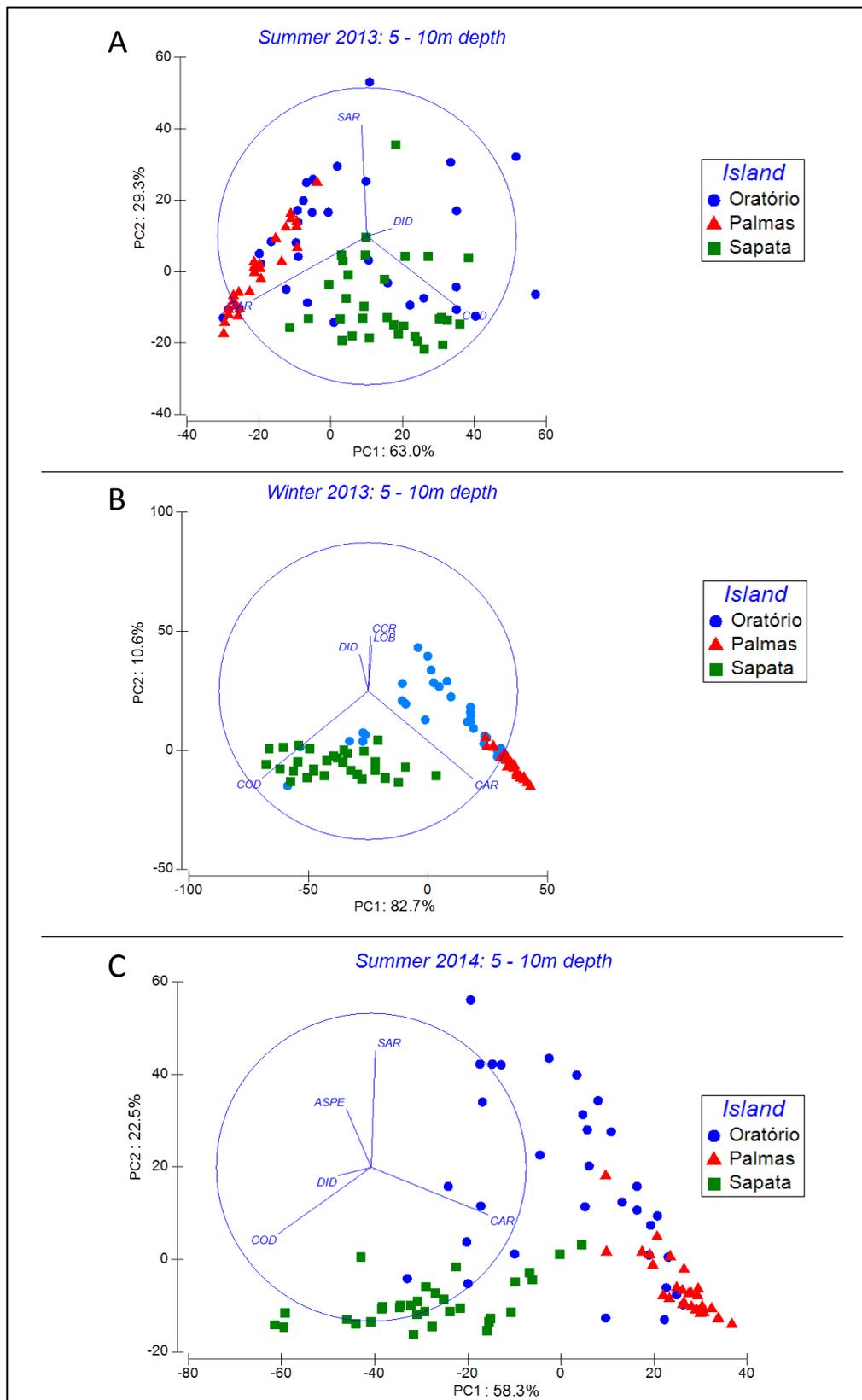


Fig. 11. Principal components analysis of the dominant taxa of the lower assemblage (5 – 10 m depth), from (A) summer of 2013, (B) winter of 2013, and (C) summer of 2014. Blue: Island of Oratório; Red: Island of Palmas; Green: Island of Sapata. CAR: Articulated Calcareous Algae; SAR: *Sargassum* sp.; COD: *Codium intertextum*; ASP: *Asparagopsis taxiformis*; DID: *Didemnum perlucidum*; ECH: *Echinometra lucunter*; CCR: Encrusting Coralline Algae; LOB: *Lobophora variegata*; ASPE: *Asparagopsis taxiformis* as epiphyte. Ordinations based in Bray-Curtis dissimilarities.

Univariate Analyses

Shallower Interval (1 – 5 m depth)

Table 6 shows the results for ANOVA, which tested for spatial differences in the cover of the dominant species and morphological groups, in all sampling periods. Table 7 presents the estimates of variance associated with each scale for those groups, along with their respective contribution in percentage.

Summer of 2013: Articulated Calcareous Algae presented significant variation on the scales of Island and Site (Table 6), with most of overall variability associated with the larger (Table 7). The barnacle *Megabalanus* sp. showed significant variation on the scale of Sector (Table 6), the only scale with positive overall variability, as revealed by the variance components (Table 7). Residual variation (among replicate units) was higher than variation on any other scale for all taxa (Table 7).

Winter of 2013: significant variability was found on the scale of Island for *Asparagopsis taxiformis* and *Sargassum* sp. (Table 6), and variation on this scale was higher than in all other scales for all the biological units, except for *Megabalanus* sp. and *Sargassum* sp. (Table 7). In spite of *Megabalanus* sp. presenting most of its variation on the scale of Sector (Table 7), this scale was not significant for any biological unit (Table 6). The scale of Site was significant for Encrusting Coralline Algae, *Megabalanus* sp. and *Sargassum* sp. (Table 6), and the latter presented most of its variation on this scale (Table 7). The scale of Meters was significant only for *Asparagopsis taxiformis* (Table 6). Residual variation was higher, followed by variation among islands, for almost all taxa (Table 7). The exceptions were Articulated Calcareous Algae and *A. taxiformis*, which presented higher variation on the scale of Island.

Summer of 2014: significant variation was found only for the Articulated Calcareous Algae, on the scale of Site (Table 6). However, variance components showed that, for both Articulated Calcareous Algae and *A. taxiformis*, overall variation was higher on the scale of Island (Table 7), followed by residual variation.

Table 6 Results of ANOVAs testing for spatial differences in mean percentage cover of abundant species in the shallower interval (1 – 5 m depth) at scales of Island, sector, site and meters. Data from the dominant biological units at all sampling periods. Estimates of multivariate variation are given for each spatial scale. Analyses based on Euclidian distances from untransformed data. Each term was tested using 999 random permutations of appropriate units. Inclination of the substrata was calculated as a covariant when this variable presented significant variation at any scale for the sampling period. *P*-values of Monte Carlo were considered.

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, ns: not significant.

Source	Island		Sector (I)		Site (Se(I))		Meters (Si(Se(I)))		Residual
	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	
Summer 2013^b									
Articulated Calcareous Algae	2152.31	10.41 [*]	206.82	0.49 ^{ns}	423.44	4.42 [*]	95.75	0.61 ^{ns}	156.92
<i>Sargassum</i> sp.	113.27	1.36 ^{ns}	83.24	0.67 ^{ns}	123.52	2.43 ^{ns}	50.78	0.64 ^{ns}	79.83
<i>Megabalanus</i> sp.	101.02	0.84 ^{ns}	120.26	6.35 [*]	18.93	0.70 ^{ns}	26.95	0.92 ^{ns}	29.17
<i>Codium intertextum</i> ^a	210.51	4.05 ^{ns}	52.00	1.75 ^{ns}	29.63	0.72 ^{ns}	41.24	1.14 ^{ns}	36.14
Winter 2013									
Articulated Calcareous Algae ^a	13900.54	33.38 ^{ns}	416.42	3.06 ^{ns}	136.08	1.32 ^{ns}	102.75	0.80 ^{ns}	128.06
<i>Codium intertextum</i> ^a	739.82	2.94 ^{ns}	251.89	2.80 ^{ns}	89.76	0.45 ^{ns}	198.26	1.44 ^{ns}	137.79
Encrusting Coralline Algae	156.26	7.68 ^{ns}	20.34	0.49 ^{ns}	41.43	4.87 ^{**}	8.51	0.61 ^{ns}	14.05
<i>Asparagopsis taxiformis</i> ^a	1935.01	25.71 ^{**}	75.26	4.48 ^{ns}	16.80	0.11 ^{ns}	153.39	3.15 ^{***}	48.62
<i>Megabalanus</i> sp. ^a	662.95	2.28 ^{ns}	290.30	4.52 ^{ns}	64.22	5.29 ^{**}	12.14	0.53 ^{ns}	22.90
<i>Tedania ignis</i>	37.63	5.10 ^{ns}	7.38	1.49 ^{ns}	4.96	0.59 ^{ns}	8.38	1.08 ^{ns}	7.74
<i>Sargassum</i> sp. ^a	272.54	44.80 ^{**}	6.08	0.08 ^{ns}	74.25	27.0 ^{***}	2.75	0.16 ^{ns}	17.08
Summer 2014									
Articulated Calcareous Algae ^a	6602.54	8.22 ^{ns}	803.25	2.31 ^{ns}	347.42	4.97 ^{**}	69.83	0.45 ^{ns}	156.39
<i>Asparagopsis taxiformis</i> ^a	3630.88	7.66 ^{ns}	474.04	3.84 ^{ns}	123.54	2.28 ^{ns}	54.29	0.81 ^{ns}	66.93
^a Variances heterogeneous									
^b Inclination of the substrate used as a covariable									

Table 7 Univariate estimates of variance associated with each scale and respective percentage contribution. Bold values represent contributions >50% of overall variability. Data from the dominant biological units of the shallower assemblage (1 – 5 m depth) at all sampling dates. MS estimates were calculated by dividing the difference between the MS of the term of interest and the MS of the term hierarchically below by the product of the levels of all terms below.

1 - 5 m depth	Island		Sector		Site		Meters		Residual	
Summer 2013		%		%		%		%		%
Articulated Calcareous Algae	60.80	23.5	0.0	0.0	40.96	15.8	0.0	0.0	156.92	60.7
<i>Sargassum</i> sp.	0.94	1.0	0.0	0.0	9.09	10.1	0.0	0.0	79.83	88.8
<i>Megabalanus</i> sp.	0.0	0.0	6.33	17.8	0.0	0.0	0.0	0.0	29.17	82.2
<i>Codium intertextum</i>	4.95	11.3	1.40	3.2	0.0	0.0	1.28	2.9	36.14	82.6
Winter 2013										
Articulated Calcareous Algae	421.38	81.5	17.52	3.4	4.17	0.8	0.0	0.0	128.06	24.8
<i>Codium intertextum</i>	15.25	8.6	10.13	5.7	0.0	0.0	15.12	8.5	137.79	77.3
Encrusting Coralline Algae	4.25	19.0	0.0	0.0	4.11	18.3	0.0	0.0	14.05	62.7
<i>Asparagopsis taxiformis</i>	58.12	42.6	3.65	2.7	0.0	0.0	26.19	19.2	48.62	35.6
<i>Megabalanus</i> sp.	11.65	21.1	14.13	25.6	6.51	11.8	0.0	0.0	22.90	41.5
<i>Tedania</i> sp.	0.95	10.6	0.15	1.7	0.0	0.0	0.16	1.8	7.74	86.0
<i>Sargassum</i> sp.	8.33	24.3	0.0	0.0	8.94	26.0	0.0	0.0	17.08	49.7
Summer 2014										
Articulated Calcareous Algae	181.23	45.7	24.49	6.2	34.70	8.7	0.0	0.0	156.39	39.4
<i>Asparagopsis taxiformis</i>	98.65	50.3	21.91	11.2	8.66	4.4	0.0	0.0	66.93	34.1

Lower Interval

Table 8 shows the spatial differences in the dominant biological units' cover individually, revealed by ANOVA. Table 9 presents the variance components associated to each scale and their respective percentage contribution for each biological unit.

Summer of 2013: significant variation was found only for Articulated Calcareous Algae, on the scale of Site and for *C. intertextum*, on the scale of Sector (Table 8). Apart from significance values, variation was higher on the scale of Island for both taxa (Table 9). Residual variation was higher than all other scales for all biological units, except for *C. intertextum*, which varied most on the scale of Island (Table 9).

Winter of 2013: Articulated Calcareous Algae presented significant variation on the scale of Sector (Table 8). However, most of the variability was found on the scale of Island, followed by residual variation, then variation on the scale of Sector (Table 9). The algae *C. intertextum* showed significant variation on the scale of Site (Table 8), and variation among islands was much higher, followed by residual variation, only then, among Sites (Table 9).

Summer of 2014: Articulated Calcareous Algae and *C. intertextum* showed significant variation on the scale of Island (Table 8), the latter also on the scale of Sector. For both taxa, variation among islands was much higher than any other scales (Table 9), followed by residual variation. *A. taxiformis* did not vary significantly on any scale and presented higher variation among replicate units (Table 9), followed, then, by variation among islands.

Table 8 Results of ANOVAs testing for spatial differences in mean percentage cover of abundant species in the lower interval (5 – 10 m depth) at scales of Island, sector, site and meters. Data from the dominant biological units at all sampling periods. Estimates of multivariate variation are given for each spatial scale. Analyses based on Euclidian distances from untransformed data. Each term was tested using 999 random permutations of appropriate units. Inclination of the substrata was calculated as a covariant when this variable presented significant variation at any scale for the sampling period. *P*-values of Monte Carlo were considered.

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, ns: not significant.

Source	Island		Sector (I)		Site (Se(I))		Meters (Si(Se(I)))		Residual
	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	
Summer 2013^b									
Articulated Calcareous Algae	5192.69	4.74 ^{ns}	1095.99	1.85 ^{ns}	592.81	3.54*	167.39	1.15 ^{ns}	145.42
<i>Sargassum</i> sp. ^a	554.86	1.41 ^{ns}	393.70	2.47 ^{ns}	159.10	1.58 ^{ns}	100.49	0.98 ^{ns}	102.50
<i>Codium intertextum</i> ^a	5079.88	4.32 ^{ns}	1177.09	19.50***	60.36	1.41 ^{ns}	42.89	0.43 ^{ns}	99.57
Winter 2013									
Articulated Calcareous Algae	22510.64	8.34 ^{ns}	2698.59	18.01**	149.84	1.20 ^{ns}	124.72	1.21 ^{ns}	103.27
<i>Codium intertextum</i> ^a	23638.04	17.98 ^{ns}	1314.38	1.76 ^{ns}	747.38	8.86**	84.38	0.81 ^{ns}	103.96
Summer 2014^b									
Articulated Calcareous Algae	12220.91	17.61*	694.06	1.84 ^{ns}	376.35	2.48 ^{ns}	151.81	1.00 ^{ns}	151.53
<i>Codium intertextum</i>	9530.98	16.28*	585.28	42.45***	13.79	0.85 ^{ns}	16.24	0.17 ^{ns}	97.93
<i>Asparagopsis taxiformis</i> ^a	2277.88	3.30 ^{ns}	690.32	2.91 ^{ns}	236.85	3.05 ^{ns}	77.63	0.79 ^{ns}	98.28
^a Variances heterogeneous									
^b Inclination of the substrate used as a covariable									

Table 9 Univariate estimates of variance associated with each scale and respective percentage contribution. Bold values represent contributions >50% of overall variability. Data from the dominant biological units of the lower assemblage (5 – 10 m depth) at all sampling dates. MS estimates were calculated by dividing the difference between the MS of the term of interest and the MS of the term hierarchically below by the product of the levels of all terms below.

5 – 10 m depth	Island		Sector		Site		Meters		Residual	
Summer 2013		%		%		%		%		%
Articulated Calcareous Algae	128.02	35.2	31.45	8.7	53.18	14.6	5.49	1.5	145.42	40.0
<i>Sargassum</i> sp.	5.04	3.9	14.66	11.3	7.33	5.7	0.0	0.0	102.50	79.1
<i>Codium intertextum</i>	121.96	41.6	69.80	23.8	2.18	0.7	0.0	0.0	99.57	33.9
Winter 2013										
Articulated Calcareous Algae	619.13	69.5	159.3	17.9	3.14	0.4	5.36	0.6	103.27	11.6
<i>Codium intertextum</i>	697.61	75.8	35.44	3.9	82.86	9.0	0.0	0.0	103.96	11.3
Summer 2014										
Articulated Calcareous Algae	360.21	64.4	19.86	3.6	28.07	5.0	0.07	0.0	151.53	27.1
<i>Codium intertextum</i>	279.55	67.7	35.72	8.6	0.0	0.0	0.0	0.0	97.93	23.7
<i>Asparagopsis taxiformis</i>	46.61	24.1	28.34	14.7	19.90	10.3	0.0	0.0	98.28	50.9

Discussion

Ecological patterns, such as scales of variation, when revealed, provide some clues about communities' structuring processes (Benedetti-Cecchi, 2001), and facilitate appropriate experimentation by the removal of statistical nuisance. However, interpreting multivariate pattern is complicated. Variation can be observed due to changes in the community composition, as well as in the relative abundance of species, even both (Benedetti-Cecchi, 2001). Evidence supports that large scale variability is compositional, and small-scale, on the other hand, is driven mostly by changes in relative abundance, especially of dominant taxa (Anderson *et al.*, 2005). Scales of variation are habitat and species-dependent, and patterns are not invariant to scale. Therefore, observed patterns cannot be generalized into a wider range of environments (Fraschetti *et al.*, 2005).

Our results revealed similar taxa as in other studies in the region. The total number of biological units that could be discriminated in the photographs was 29, as expected, according to other descriptive studies. Ghilardi (2007), in the MPA of Anchieta Island, Ubatuba, found 29 dominant species on the subtidal benthic community. Also, it was pointed out that, along rocky shores in the SE Brazil, the total number of species found in other studies, was between 32 and 70. Thus, those communities were characterized by few dominant species, which accounted for most of the cover alone (Ghilardi, 2007), as observed in the present work. Hereby, the highest number of dominant species was seven, in the shallower community, in the winter.

The dominant species encountered were expected according to records on the biodiversity of the region. All the hereby observed macroalgae were already documented by Oliveira-Filho (1977) as common

for the region. Within the Articulated Calcareous Algae of this study, the most common species were *Amphiroa fragilissima*, documented for all over the Brazilian coast, and *Amphiroa beauvoisii* and *Jania* sp., both occurring in the southeast coast. *Sargassum* sp. and *Asparagopsis taxiformis* are common from São Paulo to Espírito Santo and *Codium intertextum* from São Paulo to Bahia (Oliveira-Filho, 1977). The sponge *Tedania ignis* has already been documented in the study region, in São Sebastião, the Alcatrazes Archipelago and Ubatuba (Custódio & Hadju, 2001) and the barnacle *Megabalanus* sp. from Rio Grande do Sul to Espírito Santo (Klôh, 2001). Encrusting Coralline Algae were not classified into the species level due to difficulties in collection and identification. Although direct comparison of this group with documented species was not possible, it has already been observed by other studies in the region under the same classification (Széchy & Paula, 2000; Ghilardi, 2007).

Our results showed that the Articulated Calcareous Algae morphological group was the most abundant in all islands, also the main driver of multivariate patterns. The importance of Articulated Calcareous Algae as major components on rocky shores has been already commented by many studies. They can act as anchor taxa, persisting in the community, and containing extremely diverse assemblages of epiphytes and small cryptic invertebrates (Stewart, 1982; Kelaher *et al.*, 2001).

The coralline algae dominance can be related to environmental disturbances (Széchy & Paula, 2000). Articulated Calcareous Algae are favored by the presence of sand and sediment, due to their resistance to abrasion damage (Stewart, 1983; Steneck & Dethier, 1994; Ghilardi, 2007). Moreover, grazing has already been pointed out by many authors as a major determinant of community structure (Oigman-Pszczol, 2004). Dominance by unpalatable algae such as corallines is an indicator of strong herbivory pressure (Eston *et al.*, 1996; Ghilardi, 2007). The low relative

urchin abundance on the sampled slopes suggests that fish play a key role in structuring this community. Such process has already been mentioned by other studies which observed similar conditions (Eston *et al.*, 1986; Oigman-Pszczol, 2004). However, urchin grazing may not be discarded, once it was found to be significant in structuring benthic communities, even with low grazer density (Palacin *et al.*, 1998). The Alcatrazes Archipelago has an expressive fish biomass, and it is also a relevant location for marine turtles to feed (Leite, 2014). Gibran & Moura (2012), investigating fish assemblages, found higher species richness and larger individuals in the archipelago, in comparison to other sites in the region.

The macroalgae *Sargassum* sp. and Articulated Calcareous Algae, mostly *Amphiroa* spp. and *Jania* sp., have been identified by many studies as the most abundant, and also very important in structuring rocky shore communities along the southeast coast of Brazil (Eston *et al.*, 1986, Figueiredo *et al.*, 1994, Széchy & Paula, 2000, Amado Filho *et al.*, 2006, Ghilardi, 2007). The interspecific competition of these taxa is one of the most important processes structuring benthic communities in the region (Széchy & Paula, 2000).

Both of them were already found among dominants in several communities: In Laje de Santos, presenting also higher biomass values (Amado Filho *et al.*, 2006); In Fernando de Noronha, at many sites along different depths and distances from the coast (Eston *et al.*, 1986); In stable environments, with the replacement of *Sargassum* sp. by Articulated Calcareous Algae after the first one's reproduction (Figueiredo *et al.*, 2004); And in Anchieta Island, Ghilardi (2007) has observed a higher abundance of Articulated Calcareous Algae in the winter and of *Sargassum* sp. in the summer. This seasonality of *Sargassum* sp., in which higher values are encountered in the summer and spring, has been also

documented by other studies (Széchy & Paula, 2000; Amado Filho *et al.*, 2006).

Apart from being the most important species in abundance, in some sites along the Brazilian coast (Széchy & Paula, 2000), *Sargassum* sp. was found amongst the dominants in this study only in the first summer. Even so, it was represented by small individuals, never forming canopies, and it was much less abundant than the Articulated Calcareous Algae (ACA). This association of ACA and short *Sargassum* sp. individuals has also been observed in Laje de Santos, another insular environment in the southeast coast of Brazil, and it can be related to adaptations to strong water movements, characteristic to open ocean areas of the region (Amado Filho *et al.*, 2006).

All the significant scales of variation of Articulated Calcareous Algae were also significant for the community. For this group, in the shallower assemblage, significance was found among islands and sites in the summer of 2013 and among sites in the summer of 2014. In the lower assemblage, the group varied among sites in the summer of 2013 and among islands in the summer of 2014. The Principal Component Analysis revealed “Articulated Calcareous Algae” as an important variable determining similarity relationships among experimental units, in all cases. These observations suggest that the results of multivariate analysis of variance in this study were strongly influenced by changes in the abundance of dominant taxa.

The scales of univariate variation were taxa-specific for the other dominant species analyzed. The investigation of processes regarding particular species requires an analysis of their own spatial patterns, since each species has its own characteristic life cycle, seasonality and settling behavior. Moreover, such patterns may not be reflected in the community’s multivariate variability. Our multivariate results revealed variability in all

spatial scales but one, the one of meters. The null hypothesis, which presumed that distribution patterns would be invariant along different spatial scales, was thus rejected. Several relevant scales of variation had already been observed by other works, which, in addition to the present, confirms the complexity of marine benthic communities (Fraschetti *et al.*, 2005; Terlizzi *et al.*, 2007; Martins *et al.*, 2008).

As we previously hypothesized, variability among islands was high at all sampling periods and depths. This variation was reflected in the islands' species composition. The island of Palmas was represented mainly by Articulated Calcareous Algae, and many of the overall dominant species were absent within this island. Some of the most abundant species were present only, or mostly, in the Island of Sapata. On the other hand, the Island of Oratório presented the most heterogeneous assemblage both in species composition and in differences among its sites.

Such large-scale variation is result of multiple processes as regards organism characteristics and abiotic processes. Martins (2008) also observed high intra-island variability in the Azores and highlighted the importance of oceanic current transport, and settlement and recruitment pattern investigation in order to enlighten the processes underlying large-scale variability. Since the larger scale in the present work was in the magnitude of tens of kilometers, regional processes such as oceanic currents are unlikely suitable to explain intra-island variation, given the relative proximity of the islands. Nevertheless, the understanding of water masses' local transport should enlighten patterns of dispersion possibly affecting this community structure.

Differences among islands can also be explained by particular physical attributes influencing their assemblage distribution. Despite sampling was carried out only in slopes, the Island of Oratório has the most heterogeneous topography of all, with slopes and boulders interspersed

along the shore. This could explain the higher differences among its sites in comparison to the Island of Sapata, which is entirely flat. As already evidenced, substrate topography is a heterogeneity driver among assemblages in multiple scales (Denny *et al.*, 2004; Zawada *et al.*, 2010). This feature acts directly in community structure by offering protection, and indirectly by modifying local hydrodynamics, competition, and predation intensity (Blanchard & Bourget, 1999).

Urchin assemblages, for instance, have been associated with complex habitats, and echinoderm larvae have preferred such habitats for settlement. The presence of boulders provide shelter from predation and environmental stress for invertebrate larvae (Entrambasaguas *et al.*, 2008 and references therein). Nearby habitats with complex topography can act as sources, providing high supply of larvae and propagules, which could alter patterns in the sampled slopes by favoring the recruitment of some species, otherwise competitively inferior in such habitat. This intra-island habitat variability, promoting heterogeneity among assemblages in smaller scales, could be reflected in overall differences among islands.

The Island of Palmas also presents slopes and boulders along its shore. However, it revealed the most homogeneous assemblage. This could be due to the fact that this is the closest island from the mainland, therefore most susceptible to sedimentation. Distance from the coast is strongly associated with water transparency (Gibran & Moura, 2012). Sedimentation can be considered as a large scale process, which also affects macroalgae assemblages in small scales (Guarnieri *et al.*, 2009). Moreover, sand is an important factor influencing mat vegetation, like Articulated Calcareous Algae, and regulating the composition of the biota. It is a structural constituent of turf-like assemblages and can explain dominance by this morphological group (Stewart, 1983; Steneck & Dethier, 1994; Ghilardi, 2007).

The distance from the continent can also interfere on insular assemblages as regards human influence. Land-based anthropogenic activities can potentially alter algal assemblage structure, even from several kilometers from the coast (Tamburello *et al.*, 2012). Palmas is also far from the other islands. Distance between islands had been already correlated with differences in assemblages (Tuya & Haroun, 2006).

Dispersion may as well promote differences between islands. Since this is an isolated environment, larval retention is often low, leaving dispersion as an effect mainly of water masses (Martins *et al.*, 2008). Thus, larval supply depends on the variation of the current direction and intensity, as well as on the water turbulence, wave period, and even on the proximity of islands and their position regarding ocean currents (Scheltema, 1986; Bobadilla & Santelices, 2005; Martins *et al.*, 2008). Within an island, locally derived recruitment depends both on the local conditions of the habitat as on dispersal potential of the taxa (Johnson & Black, 2006). Islands create local currents isolating populations. Thus, locally produced larvae can be entrapped and enhance heterogeneity within an island group (Johnson & Black, 2006). Biological features also influence recruitment in insular benthic communities as result of different taxa particularities, such as the time a larvae or propagule can spend in the water column or even the ability for colonizing the substrate (Martins *et al.*, 2008).

It is well known that man is a potent vector for long distance dispersal. Larvae and propagules can be released from one place to another by means of direct transplant, species cultivation, and, most likely, organism travel through ballast water and rafting, both on ships as marine debris (Norton, 1992; Barnes & Milner, 2005). This work's community, however, is in a protected area in which direct transplantation is not allowed. Even though this potential cause is probably not applied, such

influence could have taken place before the protection, or even indirectly by species dispersion from nearby modified habitats.

Variation among Sectors (hundreds of meters) was observed in all periods in the lower assemblage, and only in the summer of 2014 in the shallower. Underwood & Chapman (1996), investigating typical open-coast shores, suggested that recruitment and post-settlement mortality can promote variability on this scale. Christofolletti *et al.* (2010) revealed that such variability can be promoted by the effect of consumers, on the sublittoral fringe of sheltered rocky shores from the same region as this. Synergistic effects of light and sedimentation maintain habitat heterogeneity on this scale in South Australian subtidal assemblages (Connel, 2005). In islands as well as in the presence of topographically complex habitats such as boulders, substrate morphology interacts with currents, producing local complex flows that can influence community structure on this scale (Banchard & Bourget, 1999).

Tidal variation could be a factor influencing variability among sectors for the shallower assemblage. The other interval presented a relatively homogeneous assemblage, despite tidal fluctuations. The shallower, on the other hand, comprises the sublittoral fringe. Overall, this assemblage was sampled and represented in the same way for all the other factors, thus permitting a sound analysis of the effect of scale. Sectors were the only one subject to tidal fluctuation during sampling. This could add variability to the system by sampling a larger portion of the sublittoral fringe during high tide.

The scale of Sites (10s of meters) was also significantly variable in the lower assemblage at all sampling periods, while in the shallower, only in the summer of 2013. Habitat complexity is an important factor explaining the variability of coral communities (Francini-Filho *et al.*, 2013) and patchiness of urchin assemblages (Entrambasaguas *et al.*, 2008) on this

scale in tropical systems. The influence of topography on hydrodynamics, shading, and predation, among other factors, has also been related with mussel bed patchiness (Erlandsson *et al.*, 2005). Recruitment has as well shown to be variable between tens of meters for other rocky shore communities (Jenkins *et al.*, 2000; Hutchinson & Williams, 2001), promoting heterogeneity into the system.

Estimates of variance revealed that residual variability (among experimental units) was high for all taxa as well as for the whole community, irrespective of depth or sampling period. This intrinsic small-scale patchiness of benthic communities has already been documented by several studies which involved multiple spatial scales (Benedetti-Cecchi *et al.*, 2001; Coleman, 2002; and see Frascchetti *et al.*, 2005 for review). Veiga *et al.* (2013) observed that residual variability in algal assemblages contributed for most of the variation in uni- and multivariate analyses for both species and functional groups.

Small-scale patchiness is a result of many local processes regulating those communities. Biological interactions are very important heterogeneity drivers, given that each species can affect the other community components' density, spatial distribution or growth (Underwood *et al.*, 1983). Foraging behavior can alter patterns of sessile prey, when grazers or predators present limited mobility (Underwood & Chapman, 1996). Predation and competition can vary and directly structure assemblages on this scale, as well as indirectly by influence of small-scale variability of environmental stressors over those processes (Menge & Olson, 1990). Recruitment can also be variable at this scale (Benedetti-Cecchi *et al.*, 2000; Jenkins *et al.*, 2000) and even interfere with other small-scale processes (Underwood & Denley, 1984).

Regional processes can also affect local dynamics, generating small-scale variability. Large-scale physical factors can modify or regulate the

importance of local factors or directly limit populations (Menge & Olson, 1990). Diversity on a local scale is dependent on the regional diversity, which enables locations with the same physical conditions to present different assemblages (Ricklefs, 1987). Dispersal can affect abundance patterns by arrival of recruits. Depending on the influx/efflux dynamics caused by different dispersal intensity, internal processes such as competition and predation can be altered (Palmer *et al.*, 1996). In other cases, when dispersal and settlement are uniform, those post-settlement processes create small-scale variation (Coleman, 2002).

The scale of Meters (less than 10m) was not variable in any season or depth. The only exception was for the algae *Asparagopsis taxiformis*, in the shallower assemblage, in the summer of 2014. Disturbance can promote patchiness and create a mosaic of development stages (Ghilardi, 2007). The high values of residual variability showed that the sampling units, when compared individually, are heterogeneous. However, when analyzed in groups, they presented no variation. This suggests that those processes creating small-scale variability are already homogeneous in a few meters. This scale is large enough so the effects of such processes, like recruitment, foraging behavior and competition are, in average, equal within its limits. For differential effects of environmental conditions such as wave action and topographic heterogeneity, this scale is too small so heterogeneity could be promoted.

As already mentioned as a heterogeneity driver for many of the scales observed, recruitment is an important mechanism in determining marine benthic community structure. Patterns of recruitment are much variable and can modify the intensity and outcome of post-settlement processes just by varying the abundance of recruits in a community (Underwood & Denley, 1984). For instance, recruitment density reduces the importance of competition (Menge & Olson, 1990), as well as alters the

foraging efficiency of grazers as regards timing and intensity of algal recruitment (Benedetti-Cecci *et al.*, 2000). As previously mentioned, this process has been documented as promoting variability in many spatial scales, including the ones hereby investigated. Jenkins *et al.* (2000) had observed significant variation in the recruitment of barnacles among tens and thousands of meters, which can be compared to the present sites and islands. They observed also high values of variability between replicates. Benedetti-Cecci (2000), also investigating barnacle recruitment, found considerable variability both in regional scale as among quadrats. Hutchinson & Williams (2001) observed variability in recruitment of tropical rocky shore communities at the scales of meters and tens of meters.

Norton (1992), in a review, addressed the principles of dispersal in macroalgae, in which many possible factors influencing this process were identified. Most propagules are generally small, and their motility is irrelevant compared with water motion influence. Water flow varies with depth and substrate topography, causing dispersal dependency on the water condition at the time of propagule release. Biological features, such as propagule morphology, survival capacity, parental plant height, and drifting reproductive capacity, may as well influence the distance of recruitment of a propagule from the moment of release. In summary, the propagule shadow model was proposed to explain general patterns of macroalgae dispersal. The model states that propagules concentrate mainly near the source site, presenting gradual decrease as distance increases (Norton, 1992). Experimentation on this model revealed that less than half of the observed dispersion patterns can be explained by seed shadows (Bobadilla & Santelices, 2005). Thus, other already mentioned factors are most likely to influence macroalgae dispersal.

For invertebrates, the reproductive strategies are many. Apart from direct developers with non-pelagic development, three types of pelagic

larvae are known: lecithotrophic larvae, which depend on their own reserves in their planktonic phase; planktotrophic larvae with long pelagic life, which feed from the plankton and grow in this life stage. The latter constitutes the majority of tropical invertebrate species; at last, planktotrophic larvae with short pelagic life, which feed from, but not grow in the plankton (Thorson, 1950). In insular systems, there is uncertainty concerning the relative role of self-recruitment versus widespread dispersal. However, an increasing amount of evidence shows genetic differentiation between island and mainland populations, as well as island populations among themselves, suggesting a great deal of self-recruitment in those environments (Bell, 2008).

Despite both depths presented algae dominated assemblages in the present study, the shallower community also comprises invertebrates among its dominants. Those different dispersal abilities of species can be a factor explaining the different patterns observed among strata. Depth and other factors such as light and bottom inclination are strong drivers of benthic assemblage structure (Francini-Filho *et al.*, 2013). Effects of light penetration were not accounted for, thus further experimentation would be required to reveal its relevance in this assemblage's structure. However, light intensity does seem as an unlikely driver of this variation, given the proximity of both strata. Substratum inclination, on the other hand, was measured and analyzed as a covariate. Therefore, its effects were considered and excluded from the analysis of horizontal variation. However, vertical comparisons were not directly analyzed, but only the resulted patterns of different depths, which leave inclination as a possible factor driving heterogeneity among strata. Other environmental gradients and biotic factors, such as water motion, temperature, salinity, presence and abundance of predators and larval preferences, are directly or indirectly

related with depth, also explaining differences (Entrambasaguas *et al.*, 2008).

The shallower assemblage has greater influence of wave action and tidal movements, which could probably better explain the different patterns between depths. The frequent disturbance generated by water movements is a factor that adds variability to this system. It is well known that rocky shore communities are strongly influenced by wave exposure (Burrows *et al.*, 2008). The macrobenthos structure in the continental shelf of the present study region had already been related to hydrodynamic patterns (Soares-Gomes & Pires-Vanin, 2003). Significant variation among algal and morphological group assemblages has been related to differences in wave exposure. This process generates continued mechanical stress to which only morphologically adapted species can resist (Tuya & Haroun, 2006).

Consumers are more affected by water turbulence than prey (Menge & Olson, 1990), what could explain the higher abundance of filamentous, more palatable, algae and invertebrates in the upper assemblage. Moreover, that could also be due to the fact that water motion enhances nutrient uptake, remove epiphytes and facilitates light absorption (Tuya & Haroun, 2006), thus favoring those species. In the Canarian Archipelago, Tuya & Haroun (2006) documented higher presence and abundance of frondose species in the exposed locations. Disturbances like this promote a non-equilibrium state in the community, interrupting the competitive process by renewing a limiting resource. Therefore, it can maintain diversity by chance replacements, and allow resource utilization by lower competitors (Levin & Paine, 1974; Connell, 1978). This could explain why the shallower interval also comprises more biological units in the dominant assemblage.

The total number of biological units was higher in the winter, for both depth intervals. This can also be related to water movements, once the hydrodynamic patterns in the study region are seasonal. During the summer, the South Atlantic Central Water (SACW) penetrates the continental shelf into the coast, creating a thermocline. In the winter, this water mass is retracted and the study region is influenced only by the Coastal Water, which is warmer and more saline. Furthermore, the winter is characterized by cold fronts that generate bottom turbulence and waves with higher amplitude (Castro-Filho *et al.*, 1987; Soares-Gomes & Pires-Vanin, 2003; Leite, 2014), which can maintain higher diversity through increased disturbance in this season. Diversity is a balance of large-scale, regional and temporal processes that add species to the community with excluding processes, such as predation, competitive exclusion or stochastic variation of the community (Ricklefs, 1987). The water action disturbance, in this case, may act stronger than other processes in determining the balance of species loss and addition.

For multivariate data, the shallower community revealed inconsistent patterns of distribution through time as regards smaller scales, other than Islands. Meanwhile, the lower community presented many scales of variation, which were the same in all sampling periods. The stronger influence of water action in the winter may also explain why the shallower assemblage was not significantly variable in scales smaller than islands. This stratum is more influenced by water movements and such disturbance may act equally within an island, decreasing heterogeneity in those smaller scales. With less influence of frequent physical disturbance in the lower strata, other processes acting together may have greater influence on structuring this community, thus maintaining high heterogeneity in many scales. Such processes, operating in all examined scales, were already

discussed, and their seasonally variable and synergistic influence difficult the affirmation of causality without further experimentation.

Among these processes, grazing is considered a major biological interaction regulating rocky shore communities (Kaehler & Williams, 1996). Urchins have unselective grazing on new settlers and can significantly control and affect distribution limits of algae and patterns of recolonization on disturbed patches (Guarnieri *et al.*, 2009). These effects are also temporally variable, and respond to the variability in the reproduction period and recruitment of algae, as well as to physical factors, which mediate foraging activity (Benedetti-Cecchi *et al.*, 2000). The study region comprises the last and greater fish biomass still in good conservation state (Leite, 2014). Gibran & Moura (2012) observed lower fish richness in colder areas, below the thermocline. Fish grazing, structuring those assemblages, may also explain differences between depths and the variation of patterns across sampling periods, given that water stratification varies along the seasons.

The periods of sampling of this study represent a singular measure of those variables in two contrasting seasons. Therefore they don't reveal the seasonal variation of these communities. To truly understand the distribution patterns and their temporal variation, further work is required with appropriate replication both in space and time.

Despite the causal processes hereby mentioned are recognized as important in community structuring, they cannot be generalized to all systems and environments. The majority of studies regarding them were performed in temperate intertidal habitats. Underwood and Denley (1984) reviewed major statements about deterministic processes in classic manipulative studies and pointed out that some caution is required when generalizing them to other systems, even with similar conditions. There is a large number of processes regulating marine community structure at once,

complicating the interpretation of multivariate patterns without further experimentation (Benedetti-Cecchi *et al.*, 2001). Ecological processes may also generate non-random distributions just by chance. Distribution patterns can be associated to a statistical origin, instead of being a result of a direct process. Therefore, observed patterns can be simply empirical descriptions instead of evidence of ecological processes (Ghilardi, 2007).

It was not in the scope of this study to test and determine causal processes structuring those communities. Our results allowed inference-making about possible structuring processes, based on comparisons with manipulative studies providing similar scales. Detection of those natural scales of spatial variability can provide insights to future experimental work regarding those processes and to monitoring implementation within the Ecological Station of Tupinambás.

To preserve or restore the patterns of variation of pristine assemblages, the establishment of criteria which defines appropriate references for those patterns is required (Benedetti-Cecchi *et al.*, 2003). Monitoring stations are urgently needed to fulfill knowledge gaps (Turra *et al.*, 2013). When meaningful ecological variables and appropriate sampling designs are identified, ecology will be more successful in solving environmental problems (Benedetti-Cecchi *et al.*, 2013).

Spatial variability was significant between tens of meters, hundreds of meters and tens of kilometers. All of those scales must be incorporated in the sampling of monitoring initiatives in the Ecological Station of Tupinambás. At the present day, resources could be focused in replicating starting from 10s of meters to larger scales, not requiring effort direction to sampling smaller scales. However, environmental impacts may increase variation on small spatial scales (Coleman, 2002), as a result of stress in the environment (Warwick & Clarke, 1993). Therefore, documenting also the scale of meters may be useful for future comparisons. The importance of

enough sampling units must be taken into consideration to compensate for the high residual variability of marine benthic communities.

All the sampled islands are very different among themselves, demonstrating high variability of insular communities, even in the same region. This clarifies the necessity of monitoring a group of islands rather than focusing in one, even considering a singular archipelago. Assessing a larger number of islands in the future will provide more insights about insular assemblages and regional processes, besides aid in the identification of their representation within MPAs.

Landscape variability must also be taken into consideration. Spatial heterogeneity should be considered as criteria for the design and implementation of MPAs (Benedetti-Cecchi *et al.*, 2003). Parameters in this level may be better predictors of assemblage structure, and assessing habitat types will benefit reserve management (Huntington *et al.*, 2010). Investigating scales of variation in a wider range of habitats, such as boulders and exposed shores, will provide complementary information about distribution patterns. This will aid even more the development of experimental and monitoring sampling designs, as well as the evaluation of effects of reserve and of temporal changes in the community. Assessing habitat distribution requires integrated baseline studies and allows the identification of biodiversity hot-spots and of valuable habitats in terms of ecosystem services (Turra *et al.*, 2013). The enlightening of habitat types and their heterogeneity will help identifying their representativeness in MPAs, providing baselines for future management and conservation plans.

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