

Marina de Oliveira Fernandez

Estrutura latitudinal e temporal de assembleias
de cnidários bentônicos em placas de
recrutamento em dois portos da costa brasileira

Latitudinal and temporal structure of benthic
cnidarians assemblages on recruitment panels
in two harbors of the Brazilian coast

São Paulo

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Orientador: Prof. Dr. Antonio Carlos Marques

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INTRODUÇÃO GERAL

Estudos da biodiversidade focam diversas escalas espaciais, em que fatores diferentes variam (Menge & Olson, 1990). A latitude, e seus fatores associados, é considerada como uma variável importante que influencia a estrutura e a dinâmica de comunidades biológicas nos tempos evolutivo e ecológico (Willig *et al.*, 2003). É clássica a hipótese de um gradiente de aumento da riqueza com a diminuição da latitude (*e.g.*, Hillebrand, 2004a, 2004b). Esta influencia também interações bióticas locais em comunidades epifaunais marinhas (Schemske *et al.*, 2009; Freestone & Osman, 2011; Freestone *et al.*, 2011).

Latitudes diferentes modulam graus de sazonalidade, a qual é menos definida em latitudes menores. Como ambientes heterogêneos tendem a ter maior heterogeneidade de espécies (Ellingsen & Gray, 2002), variações temporais são também importantes na caracterização da composição de comunidades (Magurran, 2007). Entretanto, a variação na composição de espécies depende da forma como estas espécies lidam com a variabilidade ambiental (Pandit & Kolasa, 2012), podendo adotar habitats ótimos temporalmente transitórios (Rosenzweig, 1995).

Padrões de biodiversidade resultam de processos agindo em indivíduos e comunidades, e podem ser melhor caracterizados quando estudados em escalas espaciais mais amplas (Fowler-Walker *et al.*, 2005; Leichter & Witman, 2009). Comunidades marinhas epifaunais estão estruturadas por vários fatores físicos e bióticos interagindo em escalas espaciais variáveis (Menge & Olson, 1990; Bertness *et al.*, 2001; Denny & Wetthey, 2001). Padrões de comunidades locais provavelmente resultam de uma soma de processos atuando desde escalas amplas até locais (Connell & Irving, 2009). Estimar em que medida processos locais influenciam a variação da comunidade facilita a detecção de padrões entre regiões. Comunidades locais com ampla variação podem ter processos locais atuantes tão importantes quanto processos de larga escala, enquanto uma maior variação entre regiões sugere padrões em uma escala espacial maior, superando variações locais (Connell & Irving, 2009). Assim, experimentos temporais em diferentes latitudes são uma forma de abordar hipóteses relacionadas à estrutura de comunidades.

O recrutamento é o processo que se segue ao assentamento larval, metamorfose e sobrevivência até a observação (Keough & Downes, 1982). O suprimento larval, variando no espaço e no tempo (Roughgarden *et al.*, 1988; Underwood & Keough, 2001), tem um papel importante no desenvolvimento e manutenção de comunidades bentônicas (Rodríguez *et al.*, 1993; Underwood & Keough, 2001), assim como padrões de ocupação do espaço nos estágios iniciais de desenvolvimento da comunidade (Sutherland, 1974). Padrões gerais também possuem um componente geográfico que depende da diversidade de espécies no ambiente circundante (Brown, 1988).

Espaço para assentamento é um recurso limitante em ambientes marinhos (Dayton, 1971; Jackson, 1977) e crucial para o estabelecimento de espécies exóticas (Stachowics *et al.*, 2002), que podem chegar a portos em cascos ou água de lastro de navios (Carlton & Geller, 1993; Wonham & Carlton, 2005) e recrutar nos píeres e pilares adjacentes (Glasby *et al.*, 2007). O estabelecimento bem sucedido de espécies exóticas, que caracteriza as invasões (Elton, 1958), é crescente em portos ao redor do mundo (Carlton, 1989; Ruiz *et al.*, 2000), e as alterações decorrentes na diversidade e dinâmica das comunidades são preocupantes (Megina *et al.*, 2012).

Este estudo foca em representantes do filo Cnidaria, cujo grupo mais rico em substratos artificiais é Hydrozoa, recrutando em estágios iniciais (Migotto *et al.*, 2001) ou posteriores (Morri & Boero, 1986) de desenvolvimento destas comunidades. Hidrozoários podem apresentar ciclos sazonais de atividade (Bavestrello *et al.*, 2006), taxas de recrutamento (Migotto *et al.*, 2001) e período reprodutivo (Gili & Hughes, 1995), primariamente acompanhando variações em temperatura (Calder, 1990). Em geral, estudos da sazonalidade de cnidários consideram as espécies individualmente (Calder, 1990; Migotto *et al.*, 2001; Bavestrello *et al.*, 2006). Estudos integrados que investiguem padrões temporais de riqueza e composição em assembleias de cnidários bentônicos em locais amplamente separados em latitude não foram conduzidos no Brasil, ou mesmo mundialmente.

O objetivo deste estudo é investigar a existência de padrões de variação temporal em duas assembleias de cnidários bentônicos em placas de recrutamento em

duas latitudes da costa brasileira e a influência de fatores locais na estrutura das assembleias.

No primeiro capítulo investigamos a existência de padrões de variação temporal de riqueza e composição em duas assembleias de cnidários em placas de recrutamento em áreas portuárias em diferentes latitudes da costa brasileira: o equatorial porto do Pecém (3°32'S) e o subtropical late Clube de Ilhabela (23°46'S), sob influência do Porto de São Sebastião.

O segundo capítulo é um estudo da influência da sazonalidade, microhabitats, interações bióticas e tempo de submersão na estrutura de assembleias de cnidários bentônicos em placas de recrutamento em Ilhabela, no canal de São Sebastião.

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A latitudinal comparison of temporal patterns of benthic cnidarian assemblage structure in harbors

ABSTRACT

Structure and dynamics of marine epifaunal communities are known to vary widely latitudinally, but the temporal component of this variation is relatively unstudied. Here we investigate how species richness and composition in the fouling assemblages of cnidarians in harbors vary temporally at different latitudes. We studied recruitment variation during four three-month periods in two harbor areas (Pecém at 3°32'S and Ilhabela at 23°46'S) separated by 20° latitude in Brazil. We found that (1) species richness follows the latitudinal gradient and benthic cnidarian assemblages are more speciose at Pecém, the more tropical location; (2) composition of the assemblages varies greatly over time, but is more constant at lower (equatorial) latitudes, and where variables, seems to be a consequence of greater variation in temperature at higher (tropical to subtropical) latitudes; (3) different taxa are more important for their role in assemblage structure at each site. This study highlights the importance of a temporal perspective in understanding community dynamics, and contributes to the understanding of the importance of scale in determining patterns of marine communities.

RESUMO

A estrutura e dinâmica de comunidades marinhas epifaunais variam amplamente com a latitude, mas o componente temporal desta variação é pouco estudado. Investigamos como riqueza e composição de espécies de assembleias de cnidários de substratos artificiais em portos varia temporalmente em diferentes latitudes. Estudamos variação no recrutamento ao durante quatro trimestres em duas áreas portuárias (Pecém a 3°32'S e Ilhabela a 23°46'S) separadas por 20° de latitude no Brasil. Verificou-se que (1) a riqueza de espécies segue o gradiente latitudinal e assembleias de cnidários bentônicos são mais ricas no Pecém, o local mais tropical; (2) a composição das assembleias varia muito ao longo do tempo, mas é mais constante em baixas (equatoriais) latitudes e parece ser uma consequência de maior variação da temperatura em latitudes mais altas (tropical-subtropical); (3) diferentes táxons são mais importantes por seus papéis na estrutura das assembleias em cada local. Este estudo destaca

a importância da perspectiva temporal no entendimento da dinâmica de comunidades e contribui com o entendimento da importância da escala na determinação de padrões em comunidades marinhas.

INTRODUCTION

Spatial variation in species richness has been debated for many years (Pianka, 1966; Begon *et al.*, 1990) and includes geographical components (Schall & Pianka, 1978; Brown 1988). Latitudinal patterns are often assumed, in which habitats at lower, tropical latitudes have a greater number of species than similar locations at higher latitudes (Pianka, 1966; Rohde, 1992; Rosenzweig, 1995). This latitudinal gradient was proposed for some marine systems (Hillebrand, 2004a, 2004b), but is still debated (Valentine & Jablonski, 2010; Powell *et al.*, 2012). Understanding marine latitudinal patterns and those factors that drive them are central issues in marine biology today (Roy *et al.*, 1998; Gaston, 2000; Jablonski *et al.*, 2006; Mittelbach *et al.*, 2007; Valentine & Jablonski, 2010).

Latitude is important as an influence on structure and dynamics of biological communities over evolutionary and ecological time (Willig *et al.*, 2003). For instance, low-latitude marine epifaunal communities were suggested to be shaped mostly by local interactions (Schemske *et al.*, 2009; Freestone & Osman, 2011), while high-latitude communities are more strongly shaped by the regional species pool (Witman *et al.*, 2004; Freestone & Osman, 2011). Predation, with this reasoning, is greater in the tropics and so favors species richness (Freestone *et al.*, 2011) by promoting speciation through niche partitioning (MacArthur, 1969, Freestone *et al.*, 2011). Conversely, in less speciose temperate regions, biotic interactions seemed less important and a greater proportion of the fewer species of the larger, regional scale, was also found at the local scale (Freestone & Osman, 2011), which implies that local interactions are weaker.

Energy has been also considered an important variable influencing global variation of species richness (Wright *et al.*, 1993, Clarke 2009). The positive correlations between sea surface temperature (as a proxy for energy availability) and species richness of infaunal and epifaunal bivalves (Roy *et al.*, 2000) and benthic fauna (Macpherson, 2002) support this idea.

Indeed, temperature was proposed as the most important environmental predictor of biogeographic structure of marine benthic fauna (Belanger *et al.*, 2012).

Spatial variation in species composition is hypothesized to be a consequence of geographical distance and the environmental (Nekola & White, 1999; Tuomisto *et al.*, 2003; Soininen *et al.*, 2007a, 2007b), in which habitat heterogeneity is purported to cause species heterogeneity (Ellingsen & Gray, 2002). Temporal variation in community composition ('temporal turnover,' Korhonen *et al.*, 2010), is also important for understanding species composition of any location, but has largely been overlooked. Intensity of seasonality varies among latitudes such that marked seasonality results in warm summers and cold winters at higher latitudes (intense seasonality) while higher temperatures and little variation prevail at lower latitudes (weak seasonality).

Temporal turnover and species richness of communities are negatively correlated (White *et al.*, 2006). Also, temporal turnover depends on how species respond to environmental variability (Pandit & Kolasa, 2012), such as using temporally transient optimal habitats when available (Rosenzweig, 1995). For instance, benthic communities may have different recruitment rates (*e.g.*, peaks during summer in higher latitudes and continuous recruitment at low latitudes) or growing rates (greater growth rates during summer in higher latitudes and continuous growth in lower latitudes; Freestone *et al.*, 2009).

Recruitment (following larval settlement, metamorphosis, and survival until observation, Keough & Downes, 1982) is often associated with resource limitation as space in which to settle in marine environments (Dayton, 1971; Jackson, 1977) and a wide variety and number of benthic organisms colonize artificial substrates (Svane & Petersen, 2001). The spatially and temporally variable larval supply (Roughgarden *et al.*, 1988; Underwood & Keough, 2001) is very important for the development and maintenance of benthic communities (Rodríguez *et al.*, 1993; Underwood & Keough, 2001), as well as patterns of spatial occupancy at initial stages of community development (Sutherland, 1974). Therefore, initial colonization patterns are unlikely to be repeated, while general patterns will also have a geographic component dependent upon local species diversity and availability (Brown, 1988).

Space availability is also crucial for the establishment of nonindigenous species (Stachowics *et al.*, 2002) that can arrive on ship hulls or in ballast water (Carlton & Geller, 1993; Wonham & Carlton, 2005) and recruit on nearby man-made structures (Glasby *et al.*, 2007). Invasions (the successful establishment and increase by a nonindigenous species, Elton, 1958) are an important threat to the integrity of natural communities (Megina *et al.*, 2012). Invasive species are increasing in harbors around the world (Carlton, 1989; Ruiz *et al.*, 2000) and generating concern that these invasions alter diversity and dynamics of native communities.

Different species have different roles in community structure and a general model for community structure in relation to spatial distribution of the species is bimodal with core (abundant and widely distributed) and satellite (rare and patchy distributed) species, the latter more prone to regional extinction (Hanski, 1982). Patterns of biodiversity are results of processes acting on individuals and communities and are more easily seen over broad spatial scales (Fowler-Walker *et al.*, 2005; Leichter & Witman, 2009). With this in mind, experiments over time and at different latitudes, the approach we take here, allow us to examine several hypotheses of community structure.

Here we examine community structure of the phylum Cnidaria, animals that have diverse life cycles comprising two main stages, polyp (generally benthic) and medusa (generally planktonic) or their derived, reduced, phases (Marques & Collins, 2004). Hydrozoa is the most species-rich group of the fouling community. A comprehensive list of hydrozoans in Brazil comprises 348 species, apparently unevenly distributed along the coast, probably in part because of variable attention given each region in biological studies (Marques *et al.*, 2003). Hydroids (those in the subclasses Anthoathecata and Leptothecata; Collins *et al.*, 2006) are pervasive organisms in hard substrate communities (Gili & Hughes, 1995) and may recruit early (Migotto *et al.*, 2001) or late (Morri & Boero, 1986) with respect to the remainder of the fouling community. Cnidarians can disperse at different stages, from planula or actinula larvae with variable longevity (Sommer, 1992; Campos *et al.*, 2012), to the medusa stage (Gili & Hughes, 1995), and buds and frustules (Gravier-Bonnet, 1992), as well as being transported by floating structures, such as algae (Gili & Hughes, 1995) and ship hulls (Carlton, 1987).

Here we examine patterns of temporal and spatial variability in species richness and composition in two fouling assemblages of cnidarians in harbors at different latitudes. More specifically, we attempt to answer the following questions in equatorial-tropical and tropical-subtropical regions: (1) Is there a latitudinal gradient in species richness? (2) Does community composition change seasonally and, if so, how is that change influenced by latitude? (3) Do key-taxa play important spatio-temporal roles in structuring the assemblages?

MATERIALS AND METHODS

Study sites

Pecém harbor ($3^{\circ}32'S$, $38^{\circ}48'W$, hereafter Pecém), open since 2001 (CEARÁPORTOS, 2012) is in the state of Ceará in northeastern Brazil, with equatorial warm climate all year long, with rainy (January-July) and dry (August-December) seasons (FUNCEME, 2012). Ilhabela Yacht Club ($23^{\circ}46'S$, $45^{\circ}25'W$, hereafter Ilhabela) is in the São Sebastião channel in southeastern Brazil and influenced by São Sebastião harbor, operating since 1963 (Porto de São Sebastião, 2012). This subtropical region has warm temperate climate, seasonally with warmer summers and colder winters (Figure 1).

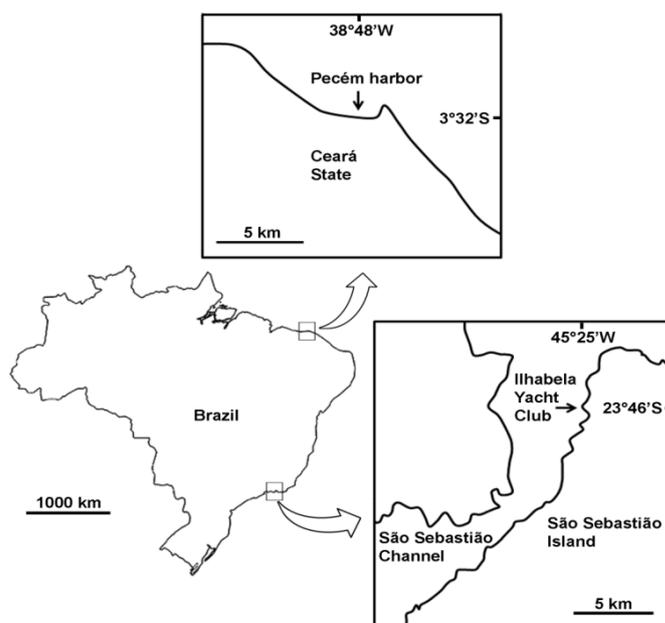


Figure 1. Locations of the study areas in Brazil, illustrating the latitudinal difference between the two locations.

The two locations are distinctly different when comparing yearly variation in sea surface temperature (SST), which is consistently greater and more constant in Ceará than in São Sebastião (Figs. 2, 3). Salinity is slightly greater in Ceará, where it decreases somewhat during the rainy season (Figs. 4, 5). Temperature and salinity data are from 1955 – 2006, from the World Ocean Atlas 2009 (Locarnini *et al.*, 2010; Antonov *et al.*, 2010, Schlitzer, 2012).

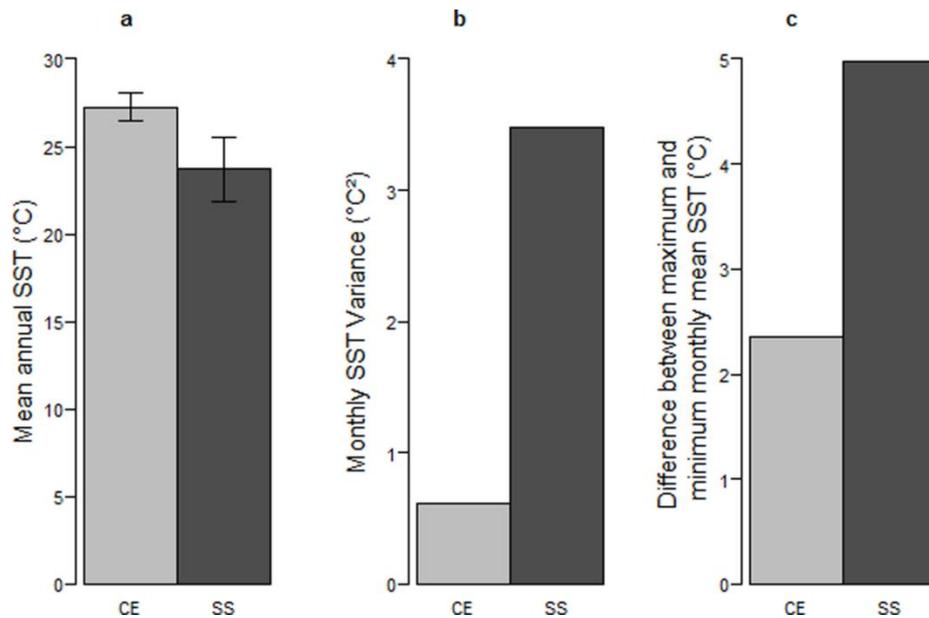


Figure 2. Sea surface temperature (SST) for equatorial Ceará (CE, light grey) and temperate São Sebastião (SS, dark grey): (a) mean annual SST in CE (27.25°C, SD = 0.78°C) is greater than that in SS (23.69°C, SD = 1.87°C) by ~ 3.6°C (bootstrap, $p \leq 0.0001$), (b) monthly mean SST variance (CE=0.61°C², SS=3.48°C²), and (c) differences between the maximum and minimum monthly mean SST in CE (2.35°C) and SS (4.97°C).

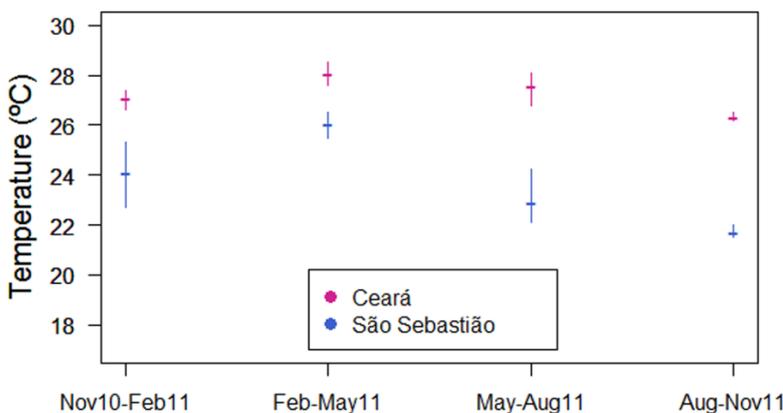


Figure 3. Ranges and mean (horizontal bar) of monthly mean sea surface temperature for the different sampling periods (see Data Sampling) in Ceará and São Sebastião (Brazil).

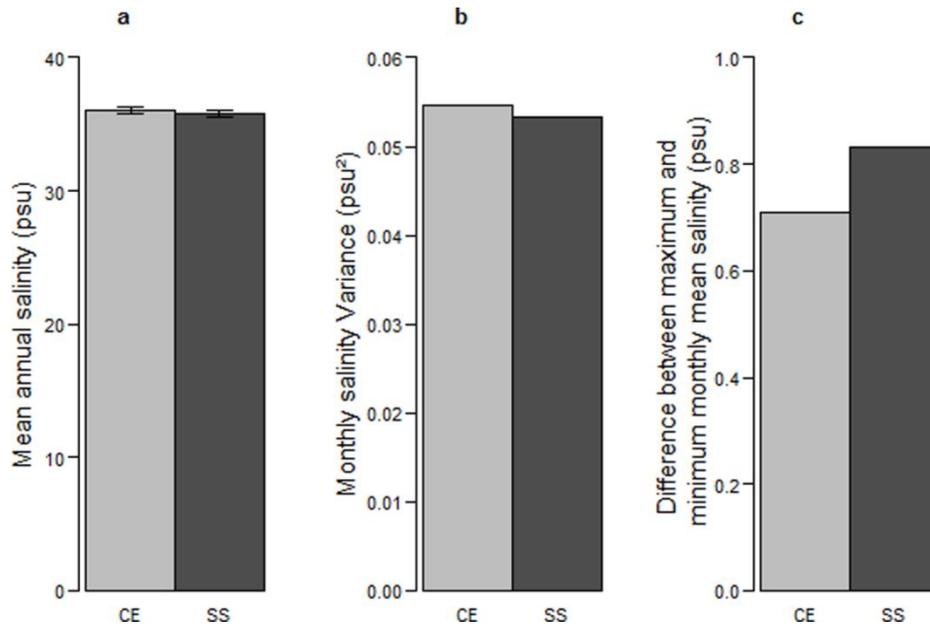


Figure 4. Surface salinity for equatorial Ceará (CE, light grey) and temperate São Sebastião (SS, dark grey): (a) mean annual salinity in CE (36.08 psu, SD = 0.234 psu) is greater than that in SS (35.78 psu, SD = 0.231 psu SD; bootstrap, $p = 0.0038$), (b) monthly mean salinity variance in (CE=0.055 psu², SS=0.053 psu²), and (c) differences between the maximum and minimum monthly mean salinity in CE (0.708 psu) and SS (0.831 psu).

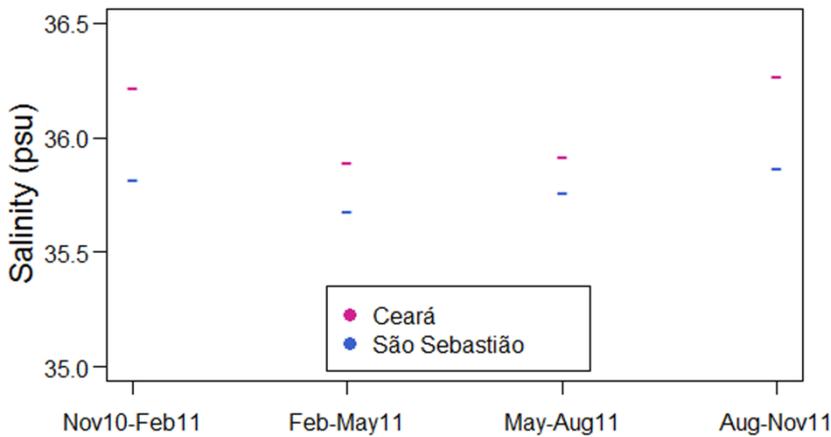


Figure 5. Mean surface salinity for the different sampling periods (see Data sampling) in Ceará and São Sebastião (Brazil).

Data sampling

We used artificial substrates to replicate habitat units and control (eliminate) microhabitat heterogeneity (Migotto *et al.*, 2001) and to investigate recruitment on a small scale and over the short term (Nandakumar, 1996; Osman & Whitlatch, 1995). Test panel replicates

(samples) were made of a sandwich of two polyethylene plates (12 x 12 cm each, times 2 is 576 cm² area for recruitment) with a 2 cm gap between plates, with both sheltered (within the gap) and exposed surfaces. Sets of plates were hung under a floating pier at Ilhabela (~3 m depth), and between pier columns at Pecém (~4 m depth at low tide). During one year (November 2010 – November 2011), 15 replicates were submerged, separated by 5 - 20 m in both study sites, where they remained for a 3 mo interval (hereafter called a period, Annex III). The four periods were November 2010 – February 2011, February – May 2011, May – August 2011, and August – November 2011, with 60 yearly samples for each site. Cnidarian species were identified on all surfaces of each sample based on descriptions in the literature (Calder, 1988; 1991; 1997; Migotto, 1996; Marques, 2001). Only species-level identified organisms and those characterized as distinct morphotypes were included in the analysis.

Statistical analysis

Analyses were all based on species presence – absence data for each sample. PRIMER v6 (Clarke & Gorley, 2006) was used to calculate sample-based rarefaction curves by permutation (Gotelli & Colwell, 2001). True species richness was estimated by Jackknife2, which considers rare species in the total richness estimates (Colwell & Coddington, 1994). These analyses were carried out for each period and the entire year in each site. All subsequent statistical analysis assume 5% significance level.

Differences between sites of the number of species per sample were compared for each period using Student's *t*-test (assumptions were correct for the *t*-test). Turnover in this context was the change in species between temporally subsequent periods (Anderson *et al.*, 2011). Estimated species richness, proportion of total richness per period and proportion of species turnover were calculated for each site. Additionally, the proportion of species turnover was calculated separately for species unique to each site and for species shared among sites. Differences among sites were estimated by bootstrap. These analyses were carried out in R (R Core Team 2012).

Temporal frequency in this study was the number of periods in which each species occurs with respect to the four sampled periods and can vary from 0.25 (one period) to 1 (all periods). Spatial frequency was the number of samples in which each species occurs relative to

the total number of test panels that were available with respect to the number of periods it occurs. We tested whether the distribution of species was different from random by randomizing the data using EcoSim v7.71 (Gotelli & Entsminger, 2012). Species were categorized as core (in all periods and spatial frequency ≥ 0.8), satellite (in all periods and spatial frequency ≤ 0.2), or rare (in only one period and spatial frequency ≤ 0.1 ; Hanski, 1982).

Multivariate analysis with Bray-Curtis similarities of presence – absence in the samples were carried out using PRIMER v6 (Clarke & Gorley, 2006) and PERMANOVA v1.0.5 (Anderson *et al.*, 2008). Comparisons of the structure of the cnidarian assemblages among periods were carried out using permutation multivariate analyses of variance (PERMANOVA; Anderson, 2001) based on 9,999 unrestricted permutations of raw data for each site. A dummy variable was added to the matrix before measuring Bray-Curtis similarities because of the undefined similarities between samples without species for Ilhabela (Clarke & Gorley, 2006). When periods were statistically different we used PERMANOVA pairwise tests. PERMANOVA is sensible to both location and dispersion of samples in multivariate space; therefore we compared homogeneity of multivariate dispersion (Anderson, 2006) between periods using PERMDISP pairwise tests (Anderson *et al.* 2008) based on 9,999 permutations, comparing the distances of observations from the centroid of the group. Differences in dispersion of the periods among sites were calculated from the mean (\pm SE) distances of observations to the centroids of the groups in the scale of Bray-Curtis similarities, and tested using Welch's *t*' because variances were unequal (Levene's test).

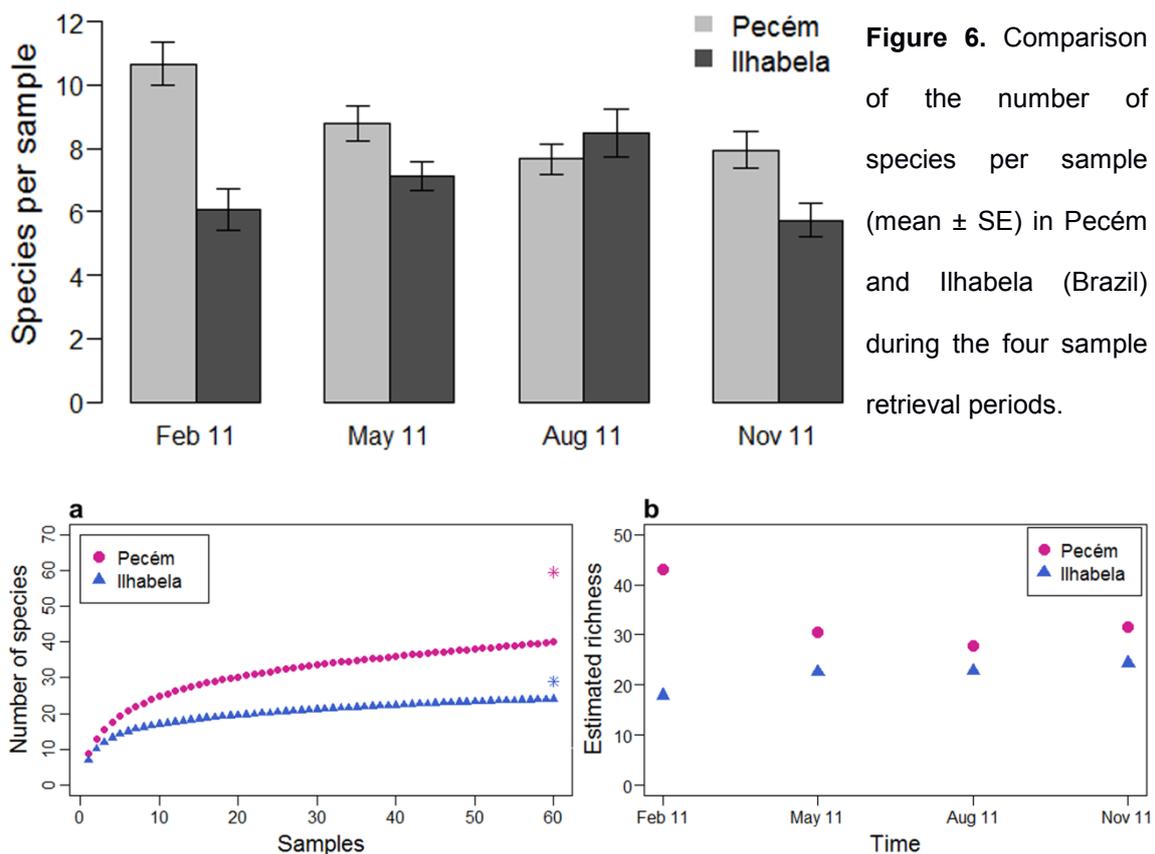
We plotted two dimensional nMDS (non-metric multidimensional scaling) (Clarke, 1993) of the 4 periods for each site. Samples without species from Ilhabela were removed from nMDS ordinations. Distances among centroids were calculated using principal coordinate axes from Bray-Curtis similarities for assemblages from each site (Anderson *et al.*, 2008), and nMDS based on the distances among centroids were also plotted.

Subsets of species that contributed most to the nMDS patterns were determined using a BVSTEP analysis (Clarke & Warwick, 2001, Clarke & Gorley, 2006), a stepwise procedure that considers the smallest subset of species whose similarity matrix has a minimum of 0.95 Spearman rank correlation with the original similarity matrix.

RESULTS

Species richness

Area available for recruitment was mostly occupied in all plates for both sites in all periods. We recorded a total of 40 and 24 cnidarian species/morphotypes for Pecém and Ilhabela, respectively (Annex I - II). Pecém had a greater number of cnidarian species per sample in 3 out of the 4 sampled periods (t -test, $p < 0.05$, with the exception of August 2011, Figure 6). Rarefaction curves (Figure 7a) do not reach asymptote and estimates of annual richness show that Pecém is more speciose (60 spp.) than Ilhabela (29 spp., Figure 7a). Estimated species richness was always greater in Pecém (bootstrap, $p = 0.0148$, Figure 7b) but sampling periods varied and species richness was greatest in February 2011. In general, greater species richness in Pecém was a consequence of more species per sample.



Spatial and temporal variation in recruitment

A large proportion of the total number of species found over all was always found in all sampling periods in both sites (Figure 8a). Pecém always had a greater temporal distribution of the total species for all periods but February 2011, although on average the values were not significantly different (bootstrap, $p = 0.0691$). Temporal turnover of species (Figure 8b) was similar in the two sites (bootstrap, $p = 0.45$), but Ilhabela had an increased turnover in species composition in May and August 2011.

Assemblage composition of the two sites was different, even though they shared 14 species (Annex I - II). Turnover for shared and exclusive species was similar in Ilhabela, while in Pecém turnover for exclusive species was greater than that for shared species (Figure 9). Sites, however, were similar in turnover of shared (bootstrap, $p = 0.1593$) and unshared (bootstrap, $p = 0.2675$) species.

Temporal patterns of occurrence are different among sites. At Ilhabela, 46% of the total number of species were present in all time periods, while at Pecém, only 33% of the species were present at all times (Figure 10).

The correlation found between spatial and temporal frequency indicates a pattern in which species with low temporal frequency have a low spatial frequency, but species with high temporal frequency may have low or high spatial frequency (for both, Pecém and Ilhabela, 10,000 iterations, $p < 0.001$, Figure 11). However, core species at Pecém (*Bimeria vestita*, *Stragulum bicolor*, *Clytia* cf. *gracilis*) were different from those at Ilhabela (*Obelia dichotoma*, *O. bidentata*). Satellite species were also different (Pecém - *Cladocoryne floccosa*, *Plumularia* cf. *strictocarpa*; Ilhabela - *Filellum* sp., *Turritopsis nutricula*). The number of rare species again was different, with 11 at Pecém and 4 at Ilhabela (Annex I-II). Except for *Stragulum bicolor*, the other core species were found at both sites (Figure 12, Annex I-II). The remaining 10 species shared by both sites had different patterns of temporal variation (Figure 13).

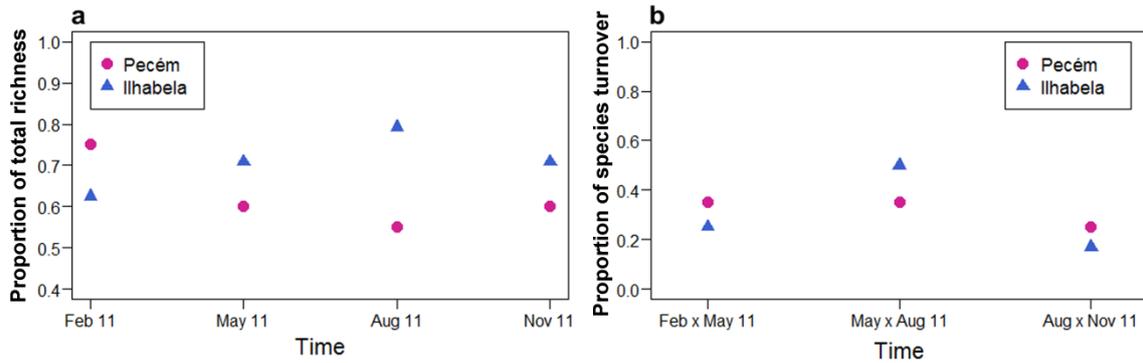


Figure 8. Comparison of total annual species richness in Pecém and Ilhabela (Brazil). (a) Proportion of total richness at each period and (b) proportion of species turnover of the total number of species.

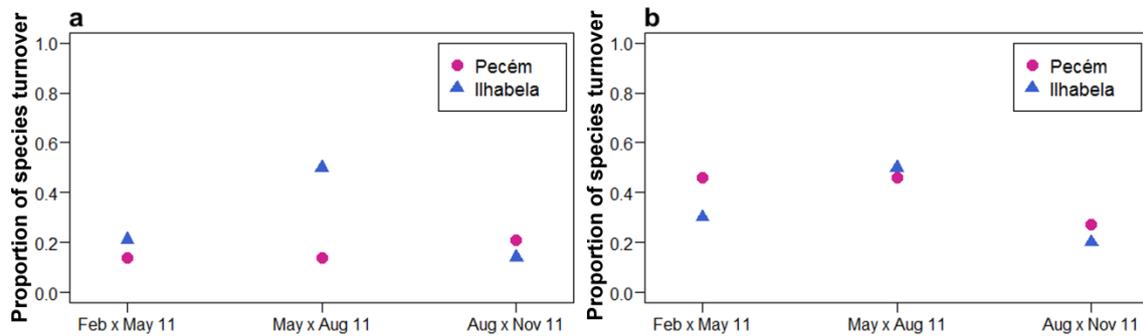


Figure 9. Species turnover in the cnidarian assemblages of Pecém and Ilhabela (Brazil), considering (a) shared species and (b) exclusive species. Data transformed to proportions of the total site richness for comparison.

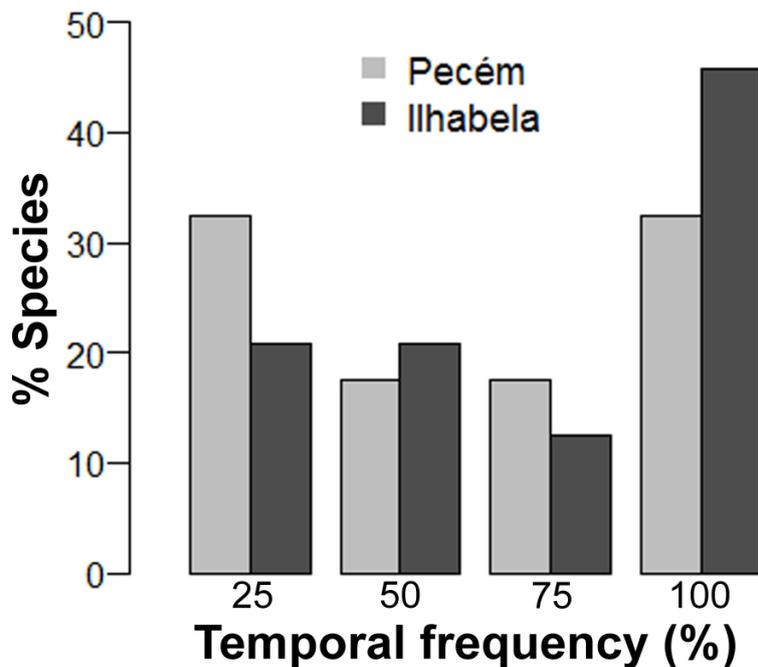


Figure 10. Percentage of species in one (25%), two (50%), three (75%) or four (100%) periods in Pecém and Ilhabela (Brazil).

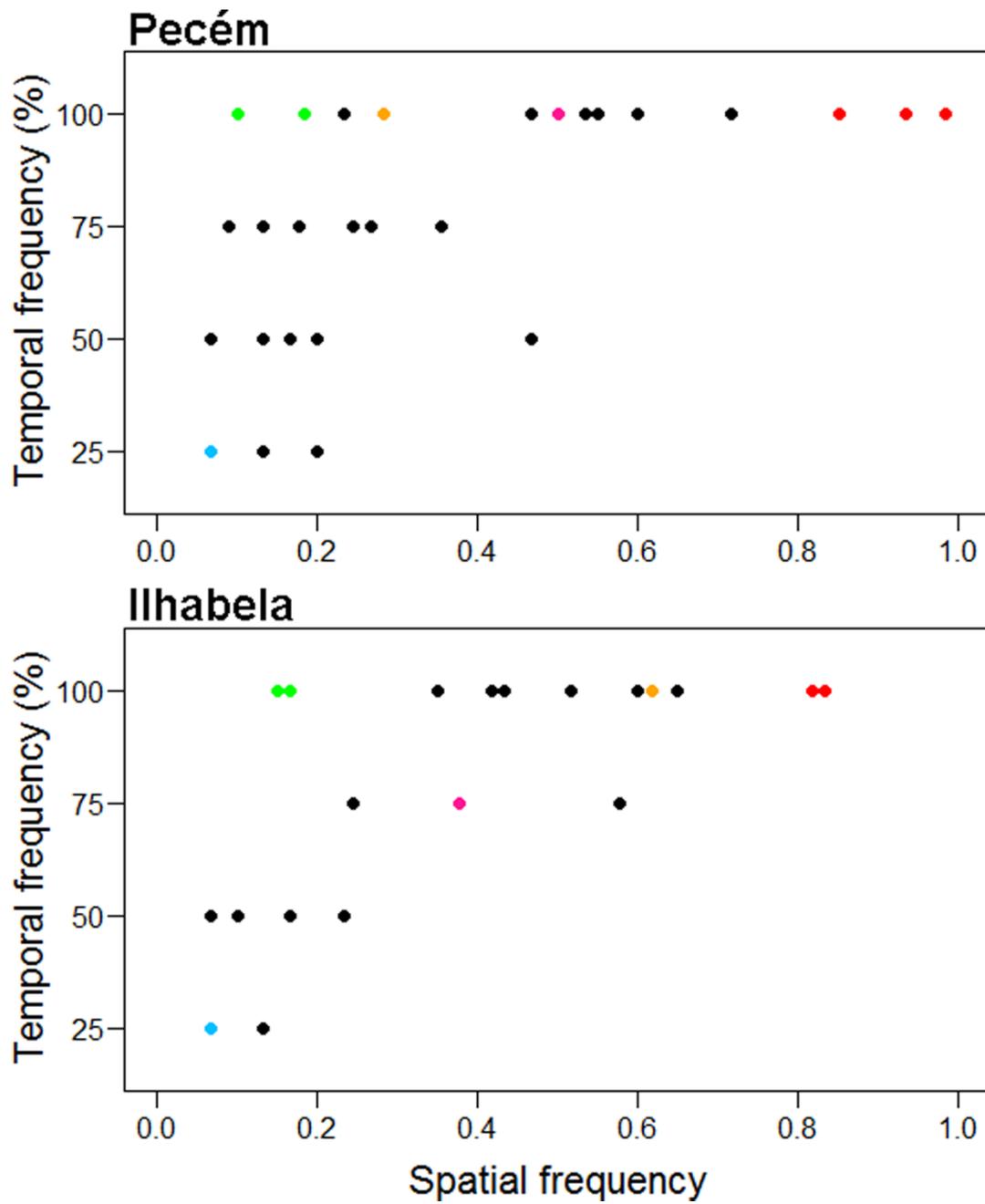


Figure 11. Correlation between spatial and temporal frequency at Pecém and Ilhabela (Brazil). Core species are indicated by red, satellite species are green, rare species are blue, core species of the other site are pink (*Obelia dichotoma* at Pecém, *Bimeria vestita* at Ilhabela) and orange (*Obelia bidentata* at Pecém, *Clytia cf. gracilis* at Ilhabela), and the remainder are black.

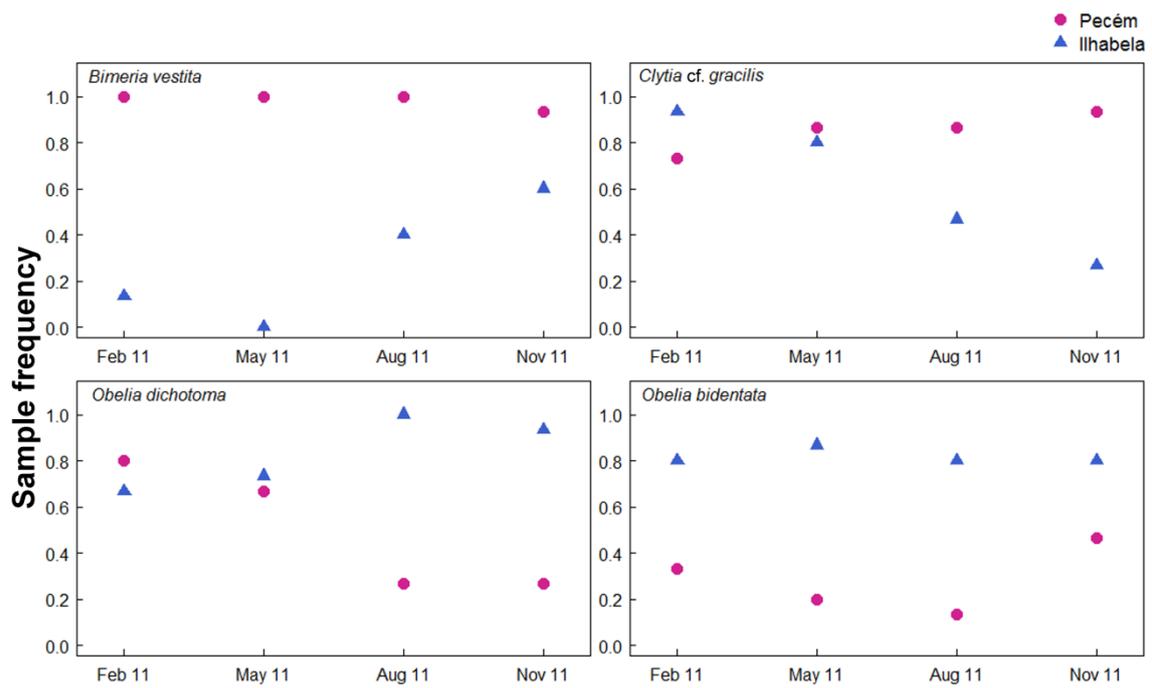


Figure 12. Frequency (proportion of samples) that four core species were found over time compared between Pecém and Ilhabela (Brazil). *Bimeria vestita* and *Clytia cf. gracilis* are core at Pecém, while *Obelia dichotoma* and *Obelia bidentata* are core at Ilhabela.

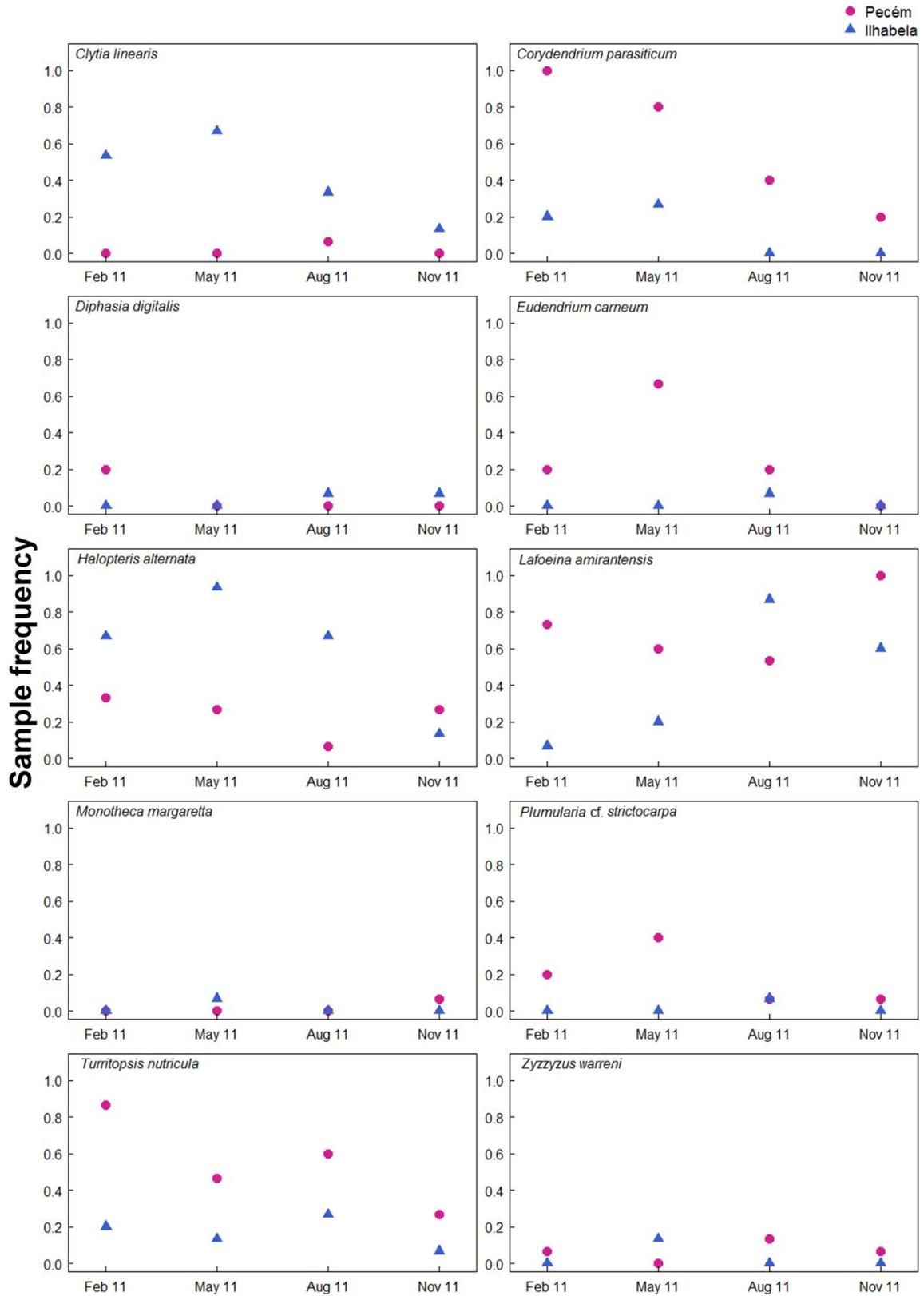


Figure 13. Frequency (proportion of samples) of the 10 non-core species shared by Pecém and Ilhabela (Brazil) over time.

The structure of cnidarian assemblages were different over time periods for both Pecém (Pseudo-F = 5.4422; P(perm) = 0.0001) and Ilhabela (Pseudo-F = 8.2268; P(perm) = 0.0001; PERMANOVA). The assemblage at Pecém was continuously different over time, while the assemblage at Ilhabela varied with respect to seasonality and the associated temperature change over time (pairwise comparisons, Table 1).

Table 1. Pairwise comparisons of cnidarian assemblage composition between periods (PERMANOVA) at Pecém and Ilhabela. Statistically significant differences are marked in grey. Note that periods were similar only in Ilhabela in February-May and August-November ($P > 0.05$).

Retrieval periods	Pecém		Ilhabela	
	t	P(perm)	t	P(perm)
February, May	16.15	0.0080	13.60	0.0798
February, August	26.65	0.0001	30.01	0.0001
February, November	30.33	0.0001	28.50	0.0001
May, August	2.08	0.0001	40.93	0.0001
May, November	26.18	0.0001	38.86	0.0001
August, November	17.61	0.0041	12.97	0.1618

The reason for these differences is that different species compositions were found at different time periods, with the exception at Ilhabela between May-November 2011, when there were different compositions within samples (PERMDISP, Table 2). At Pecém in May 2011, dispersion of species within samples was greater than that at Ilhabela (Figure 14) while dispersion was similar in the remainder.

Table 2. Pairwise comparisons of cnidarian assemblage dispersion between periods (PERMDISP) at Pecém and Ilhabela. Significant difference is marked in grey ($P < 0.05$).

Retrieval periods	Pecém		Ilhabela	
	t	P(perm)	t	P(perm)
February, May	1.52	0.1684	1.88	0.0930
February, August	1.07	0.3095	1.36	0.2914
February, November	0.23	0.8254	0.17	0.8760
May, August	0.51	0.6384	0.94	0.3710
May, November	1.25	0.2440	2.43	0.0313
August, November	0.80	0.4448	1.83	0.0770

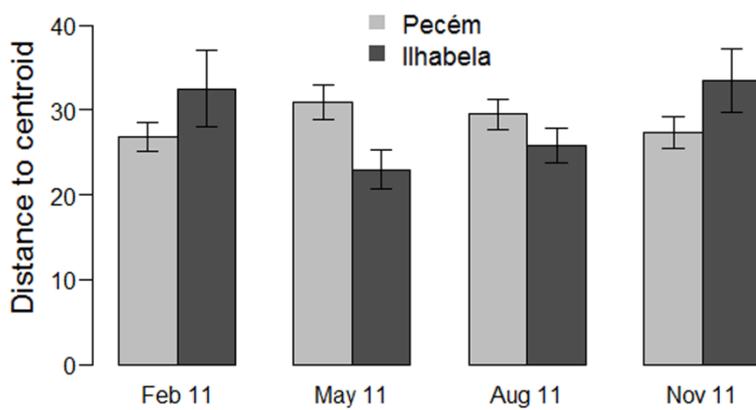


Figure 14. Comparison of dispersion (mean distances to centroids \pm SE based on Bray-Curtis similarities, PERMDISP) among sampling time periods between Pecém and Ilhabela (Brazil).

Sample structure overlaps in different periods at both sites (nMDS ordination, Figure 15). Also, February and May 2011 contrast with August and November 2011 at both sites.

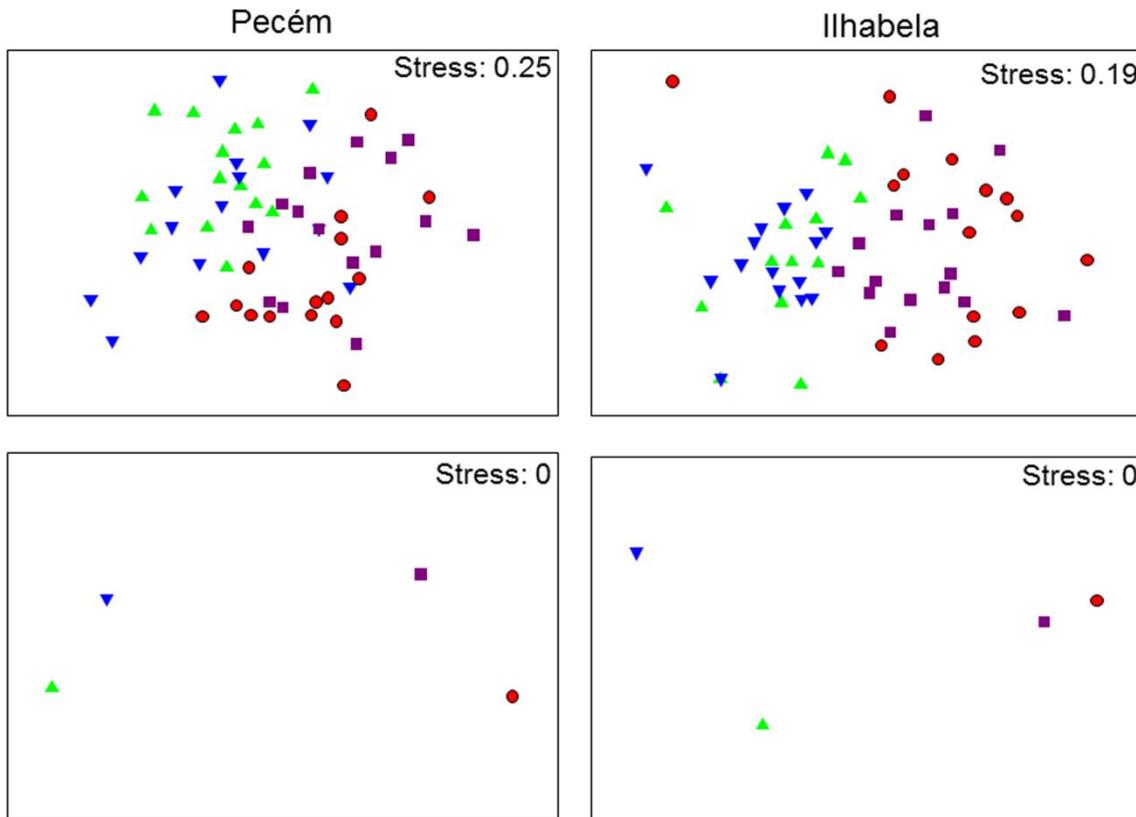


Figure 15. Comparison of cnidarian assemblages between Pecém and Ilhabela (Brazil) based on nMDS between sample periods (green triangle = February 2011, blue inverted triangle = May 2011, purple square = August 2011, red circle = November 2011). The bottom row is the distance between centroids for each period for both sites.

A subset of 18 species (45% of the total) explains nMDS temporal patterns with 0.951 correlation at Pecém, while 11 species (46% of the total) explain temporal patterns with 0.96 correlation at Ilhabela (Table 3).

Table 3. BVSTEP results on the smallest subsets of species/morphospecies generating the temporal patterns in the nMDS for Pecém and Ilhabela (Brazil). Species in bold are those shared by both sites.

Pecém	Ilhabela
<i>Bimeria vestita</i>	<i>Bimeria vestita</i>
<i>Clytia cf. gracilis</i>	<i>Clytia cf. gracilis</i>
<i>Halopteris alternata</i>	<i>Halopteris alternata</i>
<i>Lafoeina amirantensis</i>	<i>Lafoeina amirantensis</i>
<i>Obelia bidentata</i>	<i>Obelia bidentata</i>
<i>Obelia dichotoma</i>	<i>Obelia dichotoma</i>
<i>Antennella</i> spp.*	<i>Acharadria crocea</i>
<i>Bougainvillia</i> sp.2	<i>Bougainvillia muscus</i>
<i>Cladocoryne floccosa</i>	<i>Clytia linearis</i>
<i>Clytia stolonifera</i>	<i>Eudendrium caraiuru</i>
<i>Corydendrium parasiticum</i>	<i>Halecium bermudense</i>
<i>Eudendrium carneum</i>	
<i>Mitrocomium cirratum</i>	
<i>Nemalecium lighti</i>	
Octocorallia indet.1	
<i>Plumularia cf. strictocarpa</i>	
<i>Stragulum bicolor</i>	
<i>Turritopsis nutricula</i>	

**A. secundaria* and *A. siliquosa*.

DISCUSSION

Subtropical Ilhabela had fewer species of benthic cnidarians than equatorial Pecém, as predicted by theories of latitudinal gradients (Macpherson, 2002; Hillebrand, 2004b). Temporal heterogeneity was greater for tropical Pecém than subtropical Ilhabela. The greater yearly turnover at Pecém appears to reject the hypothesis of less variability in tropical latitudes due to a more homogeneous climate (although more species are available to vary at Pecém). But, while temporal turnover in Pecém was high, in Ilhabela, turnover of assemblage composition was more marked between warmer and colder months, and so was the greatest turnover that was coincident with the greatest change in temperature at both sites (Figure 2). Thus, Ilhabela was much more seasonal, while at Pecém, species composition was more diverse and constantly changing.

Competing hypotheses attempt to explain the different temporal dynamics between latitudes. On one hand, more rapid turnover for the tropics was found in a comprehensive meta-analysis (Korhonen *et al.*, 2010), which was associated with greater energy input (Brown *et al.*, 2004) and greater species diversity (Tilman *et al.*, 2006) found in lower latitudes. On the other hand, in tropical latitudes (with more constant temperatures), dry and wet seasons may cause differences in the species composition as a consequence of variation in water turbidity and nutrient supply (Boero, 1994) which may influence larval settlement and subsequent growth of the colonies. How this may influence cnidarian assemblages is unknown (Gili & Hughes, 1995). At any rate, in tropical Pecém, we did not see any clear association with the wet season, which suggests that this idea is not widely applicable.

Interestingly, at tropical Pecém, temporal turnover for species shared among sites was lower than that of exclusive species. This demonstrates the correlation between geographical and temporal distribution and agrees with the Rapoport's rule (Stevens, 1989). That is, greater environmental tolerance of species should be associated with greater latitudinal distribution of those species. Rapoport's hypothesis has often been contested, especially when distribution may be related to biogeographic factors (Roy *et al.*, 1994; Macpherson, 2003). Additionally, species have populations that vary by habitat (Koumoundouros *et al.*, 2001; Kappes & Sinsch, 2002), leading to intraspecific variation in eco-physiologies.

Although species richness was greater in Pecém, the rarefaction curve (farther from the asymptote than Ilhabela) suggests that Pecém (1) was undersampled to have precise estimates of temporal and total richness and (2) the community is underestimated in comparison to Ilhabela. Also, the proportion of the species in each period in relation to the yearly number of species was usually lower in Pecém than in Ilhabela. Thus, since estimated richness was greatest at Pecém, the true proportions are probably even lower.

Species in both sites implies that either they are widely distributed geographically, and found between the two locations, or they are only in the two sites and not elsewhere in between. If the latter, this suggests the introduction of some species in one or both harbors and, if so, temporal structure of the communities should be influenced by anthropic activities (Bertness, 1984; Reise *et al.*, 1999; Wallentinus & Nyberg, 2007). Indeed, at least one introduced species, *Stragulum bicolor* (*cf.* van Ofwegen & Haddad, 2011) plays an important role in the assemblage structure at Pecém.

Generalizations based on communities influenced by anthropic activities must be careful (Blondel & Vigne, 1993) to avoid misinterpretations about natural patterns (Steneck & Carlton, 2001). Anthropic influences on marine communities go far beyond introductions of nonindigenous species (Carlton, 1989) and can include other processes, such as pollution, fisheries and physical habitat modifications (Steneck & Carlton, 2001). All these are possibly more important in Ilhabela than Pecém because the Channel of São Sebastião has an older and more active harbor.

A recent study compared hydrozoan assemblages of harbors and natural habitats along the Iberian Peninsula, concluding that the richness of both habitats is similar though they share few species, that natural habitats are more different between each other and that the harbor species have contrasting characteristics in relation to those of natural habitats (Megina *et al.*, 2012). It is remarkable that, in harbors, the relative number of hydrozoan species without medusa (or medusoid phases), as well as large-colonied species are different in Brazil and the Iberian Peninsula (Megina *et al.*, 2012). In both, Pecém and Ilhabela, hydroid species with and without a medusa/medusoid, and species with larger or smaller, short-lived colonies, are all well represented.

The study of temporal changes of introduced species and their roles in community structure may provide better understanding of human mediated activities that influence global and temporal distributions of species in natural habitats. For instance, the cosmopolitan *Obelia dichotoma*, well known both from harbors (Millard, 1975; Ruiz *et al.*, 2000; Gaonkar *et al.*, 2010; Megina *et al.*, 2012) and natural habitats (Millard, 1975; Cornelius, 1995), is also the most frequent species in space and time in Ilhabela, and very frequent in Pecém. Nonetheless, basic questions related to the introduction status of the species or its populations remain unanswered.

Community structure variation over years is common (Sutherland & Karlson, 1977) and we recognize that this comparative analysis was restricted to a single year. Better temporal samplings, as well as the addition of comparative studies of other taxa, and different latitudes with more pronounced seasonality, may extend and further test the patterns we demonstrate here. Indeed, here we show the importance of temporal series for more accurate assessments of local richness (Magurran, 2008) and species distributions (Magurran, 2007). Assessments based on a single time sampling are not sensitive to differences in spatial and temporal patterns (Underwood & Petraits, 1993).

Our results help to understand the scales determining the patterns in which marine benthic communities are formed. We show that species composition of assemblages of benthic cnidarians varies greatly and constantly over time in lower (equatorial) latitudes while it is less speciose and varies with respect to seasonality and the associated temperature change over time at higher (tropical to subtropical) latitudes. These results highlight the importance of understanding temporal and spatial patterns in benthic communities and the difficulties to interpret patterns in increasingly human-impacted habitats.

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ANNEXES

Annex I. Species and morphospecies recorded for Pecém (NE Brazil), and their respective temporal and spatial frequencies. Species categories considered in the text are in red (core), green (satellite) and blue (rare). See text for details. **A. secundaria* and *A. siliquosa*.

Species	Temporal Frequency	Spatial frequency
? <i>Aglaophenia latecarinata</i> Allman, 1877	0.25	0.0667
<i>Acryptolaria</i> sp.	0.25	0.0667
<i>Actiniaria</i> indet.1	0.25	0.0667
<i>Actiniaria</i> indet.2	0.50	0.0667
<i>Actiniaria</i> indet.3	0.50	0.2000
<i>Actiniaria</i> indet.4	0.25	0.0667
<i>Amphinema</i> sp.	0.25	0.1333
<i>Antennella</i> spp.*	0.75	0.2444
<i>Bimeria vestita</i> Wright, 1859	1.00	0.9833
<i>Bougainvillia</i> sp.1	0.75	0.1333
<i>Bougainvillia</i> sp.2	0.50	0.4667
<i>Campanulinidae</i> indet.2	0.50	0.1667
<i>Cladocoryne floccosa</i> Rotch, 1871	1.00	0.1000
<i>Clytia</i> cf. <i>gracilis</i> (M. Sars, 1851)	1.00	0.8500
<i>Clytia linearis</i> (Thornely, 1900)	0.25	0.0667
<i>Clytia</i> cf. <i>stolonifera</i> Blackburn, 1938	0.50	0.2000
<i>Corydendrium parasiticum</i> (Linnaeus, 1767)	1.00	0.6000
<i>Diphasia digitalis</i> (Busk, 1852)	0.25	0.2000
<i>Dynamena disticha</i> (Bosc, 1802)	0.25	0.0667
<i>Ectopleura</i> ? <i>obypa</i> Migotto & Marques, 1999	0.50	0.1333
<i>Eudendrium carneum</i> Clarke, 1882	0.75	0.3556
<i>Filellum serratum</i> (Clarke, 1879)	0.25	0.0667
<i>Filifera</i> indet.	0.25	0.0667
<i>Halopteris alternata</i> (Nutting, 1900)	1.00	0.2333
<i>Lafoea</i> sp.	0.25	0.0667
<i>Lafoeina amirantensis</i> (Millard & Bouillon, 1973)	1.00	0.7167
<i>Macrorhynchia philippina</i> Kirchenpauer, 1872	0.75	0.1778
<i>Mitrocomium cirratum</i> Haeckel, 1879	1.00	0.4667
<i>Monothecha margaretta</i> Nutting, 1900	0.25	0.0667
<i>Nemalecium lighti</i> (Hargitt, 1924)	1.00	0.5333
<i>Obelia bidentata</i> Clark, 1875	1.00	0.2833

<i>Obelia dichotoma</i> (Linnaeus, 1758)	1.00	0.5000
Octocorallia indet.1	0.75	0.2667
Octocorallia indet.2	0.75	0.1333
Octocorallia indet.3	0.50	0.1333
Pandeidae indet.2	0.25	0.0667
<i>Plumularia cf. strictocarpa</i> Pictet, 1893	1.00	0.1833
<i>Stragulum bicolor</i> van Ofwegen & Haddad, 2011	1.00	0.9333
<i>Turritopsis nutricula</i> McCrady, 1857	1.00	0.5500
<i>Zyzyzus warreni</i> Calder, 1988	0.75	0.0889

Annex II. Species and morphospecies recorded for Ilhabela (SE Brazil), and their respective temporal and spatial frequencies. Species categories considered in the text are in red (core), green (satellite) and blue (rare). See text for details.

Species	Temporal frequency	Spatial frequency
<i>Acharadria crocea</i> (L. Agassiz, 1862)	0.75	0.5778
<i>Bimeria vestita</i> Wright, 1859	0.75	0.3778
<i>Bougainvillia muscus</i> (Allman, 1863)	1.00	0.6500
<i>Clytia cf. gracilis</i> (M. Sars, 1851)	1.00	0.6167
<i>Clytia linearis</i> (Thornely, 1900)	1.00	0.4167
<i>Corydendrium parasiticum</i> (Linnaeus, 1767)	0.50	0.2333
<i>Coryne</i> sp.	0.25	0.0667
<i>Diphasia digitalis</i> (Busk, 1852)	0.50	0.0667
<i>Eudendrium caraiuru</i> Marques & Oliveira, 2003	1.00	0.3500
<i>Eudendrium carneum</i> Clarke, 1882	0.25	0.0667
<i>Filellum</i> sp.	1.00	0.1500
<i>Halecium bermudense</i> Congdon, 1907	1.00	0.5167
<i>Halecium dyssymetrum</i> Billard, 1929	0.50	0.0667
<i>Halecium tenellum</i> Hincks, 1861	0.50	0.1667
<i>Halopteris alternata</i> (Nutting, 1900)	1.00	0.6000
<i>Lafoeina amirantensis</i> (Millard & Bouillon, 1973)	1.00	0.4333
<i>Monothecca margaretta</i> Nutting, 1900	0.25	0.0667
<i>Obelia bidentata</i> Clark, 1875	1.00	0.8167
<i>Obelia dichotoma</i> (Linnaeus, 1758)	1.00	0.8333
<i>Pennaria disticha</i> Goldfuss, 1820	0.50	0.1000
<i>Plumularia cf. strictocarpa</i> Pictet, 1893	0.25	0.0667

<i>Sertularella tenella</i> (Alder, 1856)	0.75	0.2444
<i>Turritopsis nutricula</i> McCrady, 1857	1.00	0.1667
<i>Zyzyzus warreni</i> Calder, 1988	0.25	0.1333

Annex III. Submersion and retrieval dates of the experimental test panels in Ilhabela Yacht Club (SE Brazil) and Pecém harbor (NE Brazil).

Ilhabela (23°46'S)		Pecém (3°32'S)	
Submersion	Retrieval	Submersion	Retrieval
4 November 2010	3 February 2011	10 November 2010	18 February 2011
3 February 2011	3 May 2011	18 February 2011	11 May 2011
3 May 2011	3 August 2011	11 May 2011	12 August 2011
3 August 2011	3 November 2011	12 August 2011	1 November 2011

Annex IV. PERMDISP dispersion results based on the average distances (\pm SE) of observations to the centroids of the groups for each period for Pecém and Ilhabela. Distances are measured on the Bray-Curtis similarities scale. Dates are relative to the retrieval of the samples.

Period	Pecém		Ilhabela	
	Average	SE	Average	SE
February 2011	26.807	1.748	32.528	4.556
May 2011	30.898	2.058	22.924	2.299
August 2011	29.509	1.813	25.780	2.006
November 2011	27.408	1.891	33.497	3.702

Structure of benthic assemblages of cnidarians in the São Sebastião channel, SE Brazil

ABSTRACT

Local marine epifaunal communities are structured by a wide variety of interacting physical and biotic factors, but few studies have investigated how these drivers of species diversity can act together on local assemblages. Here we examine how seasonality, microhabitat, biotic interactions and time of submersion influence assemblage structure of benthic cnidarians on experimental recruitment panels. We studied seasonal composition and abundance of benthic cnidarian assemblages on experimental panels during two years at Ilhabela, in southeastern Brazil, to test these influences. We conclude that cnidarian assemblages can be structured by each of these factors: microhabitat, biotic interactions, and time of submersion. Assemblages vary temporally in species compositions, but abundance is not seasonally determined. This study assess the importance of some of the factors that acting in combination influence cnidarians recruitment.

RESUMO

Comunidades marinhas epifaunais locais estão estruturadas por diversos fatores físicos e bióticos em interação, mas poucos estudos investigaram como estes direcionadores da diversidade de espécies podem agir em conjunto em assembleias locais. Examinamos como sazonalidade, microhabitat, interações bióticas e tempo de submersão influenciam a estrutura da assembleia de cnidários bentônicos em placas de recrutamento. Estudamos composição sazonal e abundância de assembleias de cnidários bentônicos em placas experimentais durante dois anos em Ilhabela, no sudeste do Brasil, para testar estas influências. Concluímos que assembleias de cnidários podem estar estruturadas por cada um destes fatores: microhabitat, interações bióticas e tempo de submersão. A composição de espécies das assembleias varia temporalmente, mas a abundância não é sazonalmente determinada. Este estudo avalia a importância de alguns dos fatores que agindo em conjunto influenciam o recrutamento de cnidários.

INTRODUCTION

Marine epifaunal communities are structured by a wide variety of interacting physical and biotic factors (Menge & Olson, 1990; Bertness *et al.*, 2001; Denny & Wetthey, 2011). Temperature (Clarke, 2009), oceanographic processes (Broitman *et al.*, 2005), larval supply (Hughes *et al.*, 2000) and species interactions (Navarrete & Berlow, 2006) are among the many drivers of species diversity acting in different spatial scales (Menge & Olson, 1990). The influence of these factors on the structure of marine assemblages is a central issue for conservation and ecology (Agardy, 1994; Benedetti-Cecchi *et al.*, 2003; Crowder & Figueira, 2006).

Variation in temperature influences marine diversity (Clarke, 2009) by its interaction with annual cycles of growth, reproduction, composition and abundance, all of which vary geographically (Coma *et al.*, 2000) and taxonomically (Keough, 1983). Another important driver is supply of larvae, as well as larval response to environmental cues prior to settling and metamorphosis (Pechenik, 1999). Larval settlement often implies selection of microhabitats as refuges, protecting the organisms against predation (Keough & Downes, 1982).

A myriad of biotic interactions are the result of the different taxa comprising the local community, with consequences from larval settlement to adult survival and reproduction (Osman & Whitlatch, 1995). Colonization of bare substrate includes initial larval settlement, metamorphosis and survival (recruitment; Keough & Downes, 1982). Recruitment is often influenced by intense competition for space (Jackson, 1977) and often results in species being overgrown by surrounding residents (Hirata, 1987; Osman *et al.*, 1989) and epibiosis by the larvae of the newcomers (Wahl, 1989). Once established, species vary in their ability to resist subsequent recruitment and to invade occupied substrate (Sutherland & Karlson, 1977; Osman & Whitlatch, 1995). Some species considered to be specialists attach exclusively on certain organisms (Osman & Haugsness, 1981). Consequently, the recruitment of a single species can influence the composition of the community (Sams & Keough, 2012).

Spatial distributions of marine species are predicted to be bimodal in that core species are abundant, widely distributed species and satellite species are rare and patchy in their distributions (Hanski, 1982). Although sampling time also has an effect on the distribution of

species, it is unclear whether time (on a proximate, short-term scale) may also generate patterns similar to those of core and satellite spatial distributions (Magurran, 2007).

Limited space for settlement in marine habitats (Dayton, 1971; Jackson, 1977) might explain why recruitment so often occurs on artificial substrates and in a wide variety of benthic organisms (Svane & Petersen, 2001). The study of recruitment on artificial panels allows us to investigate processes occurring over small time scales (Nandakumar, 1996; Bram *et al.*, 2005; Freestone *et al.*, 2009). Additionally, we may assume that recruitment dynamics on test panels is a reflection of those same processes that influence recruitment on natural substrates and for many processes associated with bioinvasion (which is nearly ubiquitous today).

As in communities on natural substrates, community structure on recruitment panels is determined by processes that influence larval recruitment and vary in space and time (Sutherland & Karlson, 1977; Roughgarden *et al.*, 1988; Nandakumar, 1996; Butler & Connolly, 1999), by initial patterns of community development (Sutherland, 1974), which varies relative to time of submersion (Bram *et al.*, 2005), and by colonization success (Keough & Downes, 1982). This complex of influences can be seen, for instance, by noting that replicates that are simultaneously submerged are often very different from each other in the assemblages they acquire (Keough, 1983).

Here we examine assemblage processes with representatives of the phylum Cnidaria. These species have diversified life cycles comprising two main stages, polyp (generally benthic) and medusa (generally planktonic) or their derived reduced phases (Marques & Collins, 2004). Hydrozoa is the largely represented group on recruitment panels. Their opportunistic settling patterns (Calder, 1991b; Migotto *et al.*, 2001) allow them to arrive in a variety of habitats and substrates where competition may be lower (Gili & Hughes, 1995). Also, rapid larval settlement and rapid growth of asexual colonies explain how hydroids are among the initial recruits on bare substrates and their habit of growing over other organisms that gradually replace the initial fauna (Boero, 1984; Migotto *et al.*, 2001). Additionally, some hydroids develop relatively large and robust colonies that can resist settlement and overgrowth by other sessile invertebrates, such as sponges, tunicates, and bryozoans (Migotto *et al.*, 2001).

Hydroids often have seasonal cycles, including activity (Bavestrello *et al.*, 2006), recruitment rates (Migotto *et al.*, 2001), and reproduction periods (Gili & Hughes, 1995), often following variation in temperature (Calder, 1990; Migotto *et al.*, 2001). Most studies of cnidarian seasonality addressed individual species and not assemblage patterns (Calder, 1990; Migotto *et al.*, 2001; Bavestrello *et al.*, 2006). Given this context, here we experimentally examine the influence of seasonality, microhabitat, biotic interactions and time since submersion on cnidarian benthic assemblage structure using recruitment panels in southeastern Brazil.

MATERIALS AND METHODS

Study site

The study was carried out at the Ilhabela Yacht Club (hereafter Ilhabela), in the São Sebastião Channel (SSC) in southeastern Brazil ($23^{\circ}46'S$, $45^{\circ}25'W$). The yacht club is near the São Sebastião harbor, in operation since 1963 (Porto de São Sebastião, 2012). The region has a subtropical climate with warm and rainy summer and cool and dry winter. The SSC is 22 km long and separates the continent from the island of São Sebastião (Castro *et al.*, 2008, Figure 1). It is influenced by Coastal Water mass (Castro *et al.*, 2008), occasionally South Atlantic Central Water mass from late spring to summer and rarely Tropical Water mass in autumn (Castro *et al.*, 2008). Currents in the SSC are primarily wind driven (Castro *et al.*, 2008). We used daily sea surface temperature data from SSC recorded at the marine biology center “Centro de Biologia Marinha”.



Figure 1. Study site in the São Sebastião Channel, Brazil.

Data sampling

We monitored seasonal recruitment of benthic cnidarian larvae on sets of experimental test panels made of a sandwich of two polyethylene plates (12 x 12 cm each, 144 cm² area for recruitment on each surface) with a 2 cm gap between plates, with both sheltered (within the gap) and exposed surfaces. Sets of panels were hung 5 - 20 m apart, under a floating pier at ~3 m depth. For two years (February 2010-February 2012), 30 panels were submerged simultaneously where they remained for three months (Annex I), for a total of eight 3 mo periods and 240 samples. Another 60 panels were maintained in the water for a year (30 from February 2010 – 2011, and another 30 February 2011 – 2012), comprising two groups of annual samples.

Cnidarian species composition was determined using one exposed and one sheltered surface on each set of test panels (each surface being a sample), for a total of 15 samples each per time period. Samples were analyzed using a grid of 144 squares (1 cm²) to estimate percent cover on the test panel for each species. Each square was ranked following Migotto *et al.* (2001), with the following categories: zero (absent), 1 (~25% covered), 2 (~50%), 3 (~75%), and 4 (100%). Total cover was estimated as the sum of the values of each square (Dethier *et al.*, 1993). Species were also noted for how they fix to the substrate in each square, as (1) epibionts, (2) directly attached to the panel surface with no overgrowth by other invertebrates, or (3) directly attached to the panel surface and in some stage of being overgrown by other invertebrates. Species were identified based on descriptions in the literature (Calder, 1988; 1991a; 1997; Migotto, 1996; Marques, 2001) and only those species identified and those characterized as distinct morphotypes were included in the analysis.

Statistical analysis

Sample-based rarefaction curves by permutation (Gotelli & Colwell, 2001) and species richness estimations by Jackknife2, considering the number of rare species in the total richness (Colwell & Coddington, 1994), were calculated using PRIMER v6 (Clarke & Gorley, 2006). Rarefaction curves were made for each year, for 3-months samples and for 1-year samples.

We calculated the proportion from total species richness found in each period, the proportion from total richness changing between consecutive periods, i.e., temporal turnover (Anderson *et al.*, 2011), and the percentage of species with different temporal frequencies

(percentage from the 8 periods in which a species occur), from one (12.5%) to eight (100%) periods.

We calculated average cover on samples relative to each species temporal frequency. We tested whether the correlation between each species average cover and its temporal frequency was randomly distributed by randomizing data using EcoSim v7.71 (Gotelli & Entsminger, 2012). Species with extreme values in this distribution were categorized as core (in all periods with the highest average cover and up to 90% of this value), satellite (in all periods with the lowest average cover up to 10% greater than that), and rare (in only one period with cover ≤ 0.001) (cf. Hanski, 1982).

All multivariate analyses were performed in PRIMER v6 (Clarke & Gorley, 2006) and PERMANOVA v1.0.5 (Anderson *et al.*, 2008) using Bray-Curtis similarities for cover. Similar weights were applied for all species after standardizing their cover by the maximum value between variables (Quinn & Keough, 2002).

Permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) was used with 9,999 permutations of residuals under a reduced model. A dummy variable was added to the matrix before measuring Bray-Curtis similarities because of the undefined similarities between samples without species (Clarke & Gorley, 2006). To compare cnidarian assemblages between periods and between inner and outer surfaces, a first PERMANOVA analysis comprised factors Time (fixed; 8 levels; with contrasts: first *versus* second year levels) and Surface (fixed; 2 levels; crossed with Time). A second PERMANOVA analysis included the 1-year panels for both years, with factors Time (fixed; 10 levels; with contrasts: all 3-month *versus* 1-year levels, 3-month *versus* 1-year levels from the first year, and 3-month *versus* 1-year levels from the second year) and Surface (fixed; 2 levels; crossed with Time). Both had 15 replicates for each combination of factors.

When we rejected the hypothesis that all periods were similar, we used pairwise tests in PERMANOVA to determine which periods differed and how so. If interactions between Time and Surface were important, we performed pairwise tests and non-metric multidimensional scaling (nMDS, Clarke, 1993) between levels of Time within levels of Surface. Otherwise, we performed pairwise tests and nMDS without the interaction. Samples without species were removed from

the nMDS ordination. Complementarily, we performed nMDS for the distances among the centroids of the periods, calculated using the principal coordinate axis from Bray-Curtis similarities (Anderson *et al.*, 2008). Differences in homogeneity of multivariate dispersion (Anderson, 2006) between periods and surfaces were evaluated by PERMDISP pairwise tests (Anderson *et al.*, 2008) based on 9,999 permutations, comparing the distances of observations from the centroid of the group.

The most important subsets of species contributing to the nMDS patterns among the eight periods were determined by a BVSTEP analysis (Clarke & Warwick, 2001, Clarke & Gorley, 2006), a stepwise selection procedure which results in the smallest species subset whose similarity matrix has a minimum correlation of $r_{\text{Spearman}} = 0.95$ with the original similarity matrix (Clarke & Warwick, 2001).

With species cover, to determine patterns of association of species with respect to surface, we used the point-biserial correlation coefficient (De Cáceres & Legendre, 2009) in R (R Core Team, 2012). This index is calculated for each species independently, so the pattern observed for one species is independent of the patterns of other species (De Cáceres & Legendre, 2009). Presences inside and absences outside a given group contribute to the strength of the association (De Cáceres & Legendre, 2009). Additionally, cover of outer and inner surfaces was compared.

RESULTS

Sea surface temperature

Sea surface temperature (SST) varied from 18.3°C to 28.8°C for the SSC during the sampling period (Figure 2).

Species richness

A total of 34 cnidarian taxa were found in the 3 mo samples summed over the two years total exposure at Ilhabela (Figure 3): 32 hydroids and 2 small, rare sea anemones. The rarefaction curve does not asymptote and the expected richness was estimated at 47 species.

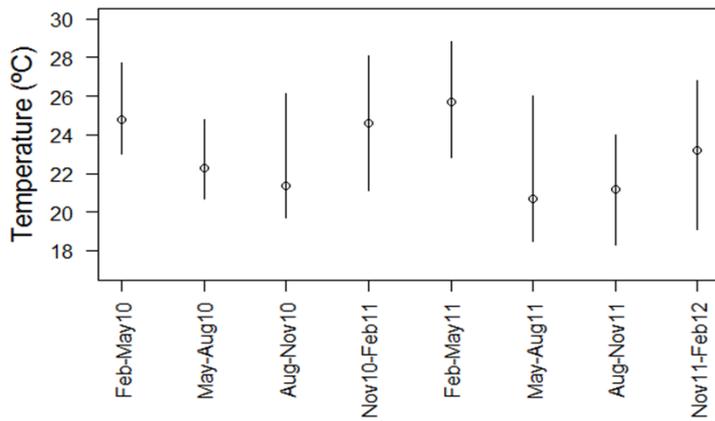


Figure 2. Sea surface temperature in the São Sebastião Channel (Brazil) by sampling periods. Circles are mean temperatures and lines include the range of values.

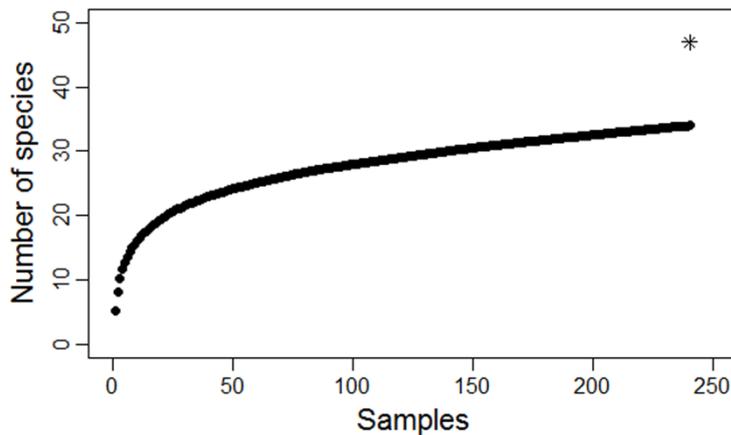


Figure 3. Sample-based rarefaction curve and estimated species richness (Jackknife2; *) for 3-month panels sampled from February 2010 to February 2012 at Ilhabela (Brazil).

Temporal patterns

Many species contributing to total richness during the two-year experiment were in all periods, especially in August 2010 (Figure 4). Species turnover oscillated along the 2 years (Figure 5), with greatest turnover during periods May-August in both 2010 and 2011.

Temporal frequencies of the species was bimodal, with the peaks for both species that occurred in only one period and for species that occurred in all periods (Figure 6). Few species were intermediate in temporal frequencies. Species infrequent in time were also less abundant, and species common over time varied from low to high abundances (Figure 7). The relationship between abundance and time was not random (10,000 iterations, $p = 0.0013$) and instead, was triangular. The extremes of the triangular distribution are one core (*Obelia dichotoma*), one satellite (*Turritopsis nutricula*) and 9 rare species (Table 1, Figure 7).

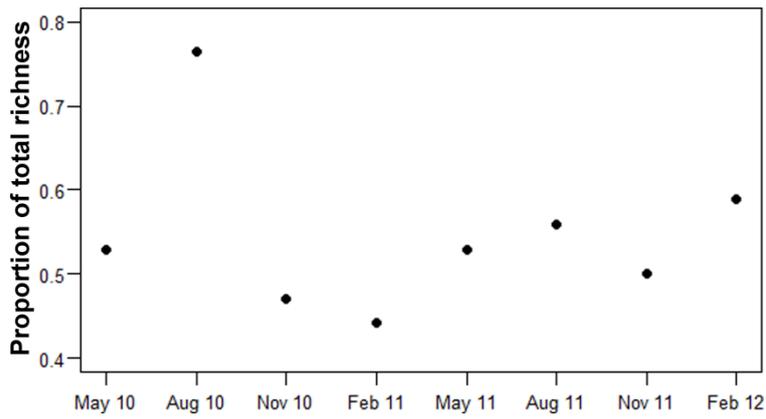


Figure 4. Proportion of species in the 2 year total observed in each sampling period at Ilhabela (Brazil).

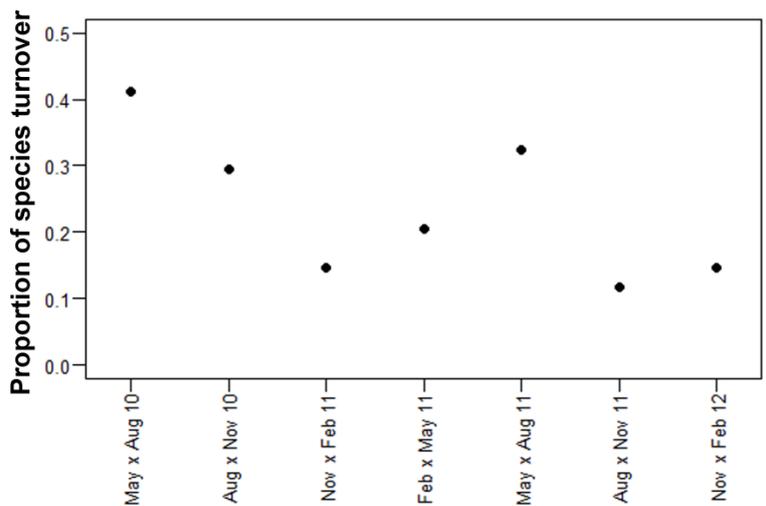


Figure 5. Species turnover in subsequent sampling periods as a proportion of the total number of species at Ilhabela (Brazil).

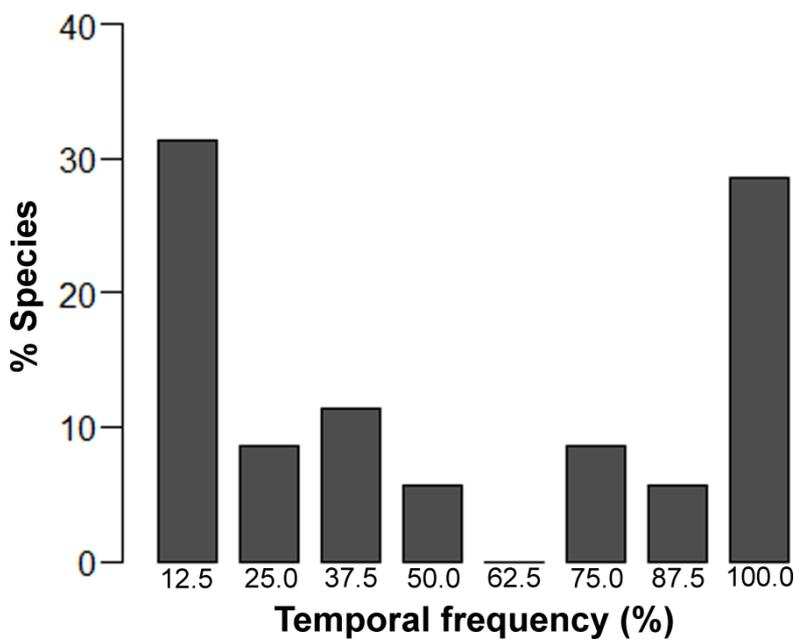


Figure 6. Percentage of species by the temporal frequency, from one (12.5%) to eight (100.0%) sampling periods, in which they were found at Ilhabela (Brazil), from February 2010 to February 2012.

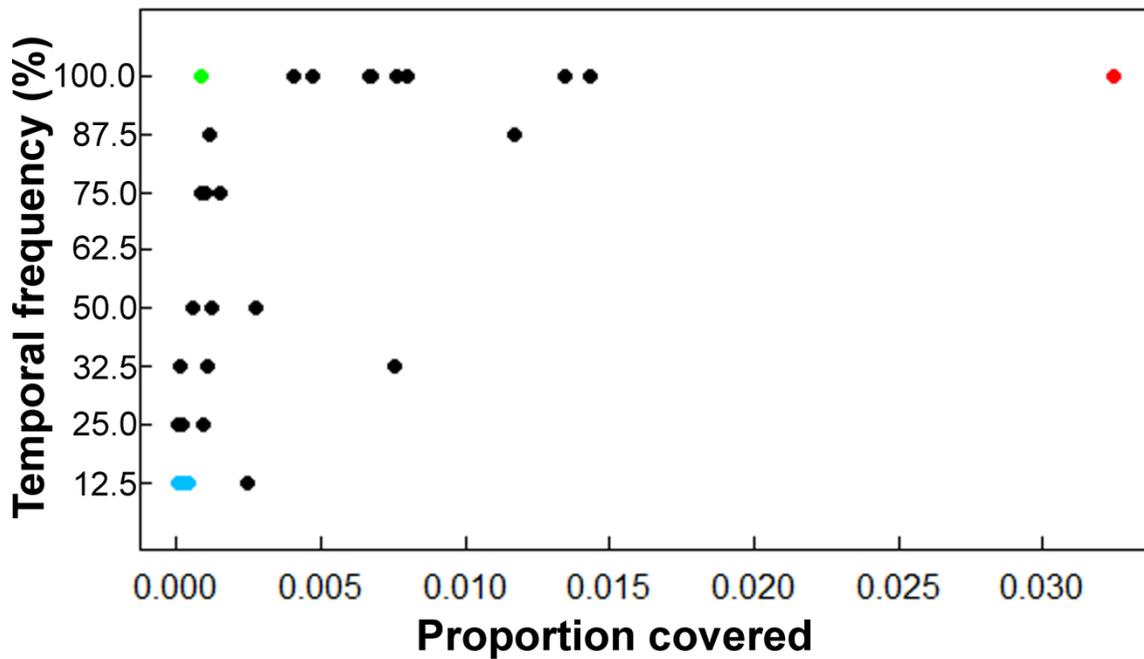


Figure 7. Relation between cover and the temporal frequency, from one (12.5%) to eight (100.0%) sampling periods, in which a species was found at Ilhabela (Brazil), from February 2010 to February 2012. The red dot is the core species *Obelia dichotoma*, green is the satellite species *Turritopsis nutricula* and in blue are nine rare species.

Table 1. Species and morphospecies recorded from February 2010 – 2012 at Ilhabela (Brazil), their respective temporal frequencies and average proportion of cover on 3-month samples. Species categories considered are red (core), green (satellite) and blue (rare).

Species	Temporal frequency	Average cover
<i>Acharadria crocea</i> (L. Agassiz, 1862)	0.875	0.0117
<i>Actiniaria</i> indet.7	0.500	0.0005
<i>Actiniaria</i> indet.8	0.125	0.0024
<i>Bimeria vestita</i> Wright, 1859	0.750	0.0009
<i>Bougainvillia muscus</i> (Allman, 1863)	1.000	0.0076
<i>Clytia</i> cf. <i>gracilis</i> (M. Sars, 1851)	1.000	0.0047
<i>Clytia linearis</i> (Thornely, 1900)	1.000	0.0067
<i>Clytia</i> cf. <i>stolonifera</i> Blackburn, 1938	0.125	0.0004
<i>Corydendrium parasiticum</i> (Linnaeus, 1767)	0.375	0.0076
<i>Coryne</i> sp.	0.500	0.0012
<i>Diphasia digitalis</i> (Busk, 1852)	0.375	0.0002
<i>Eudendrium caraiuru</i> Marques & Oliveira, 2003	1.000	0.0067
<i>Eudendrium carneum</i> Clarke, 1882	0.375	0.0011

Species	Temporal frequency	Average cover
<i>Filellum</i> sp.	0.875	0.0011
<i>Haleciidae</i> indet.1	0.125	0.0004
<i>Haleciidae</i> indet.2	0.125	0.0002
<i>Halecium bermudense</i> Congdon, 1907	1.000	0.0143
<i>Halecium dyssymetrum</i> Billard, 1929	0.250	0.0001
<i>Halecium tenellum</i> Hincks, 1861	0.750	0.0010
<i>Halopteris alternata</i> (Nutting, 1900)	1.000	0.0134
<i>Lafoea</i> sp.	0.125	0.0003
<i>Lafoeina amirantensis</i> (Millard & Bouillon, 1973)	1.000	0.0040
<i>Monothecha margaretta</i> Nutting, 1900	0.125	0.0001
<i>Obelia bidentata</i> Clark, 1875	1.000	0.0080
<i>Obelia dichotoma</i> (Linnaeus, 1758)	1.000	0.0325
<i>Pandeidae</i> indet.1	0.125	0.0001
<i>Parawrightia robusta</i> Warren, 1908	0.125	0.0002
<i>Pennaria disticha</i> Goldfuss, 1820	0.500	0.0028
<i>Plumularia</i> cf. <i>strictocarpa</i> Pictet, 1893	0.250	0.0002
<i>Sertularella tenella</i> (Alder, 1856)	0.750	0.0015
<i>Sertularia marginata</i> (Kirchenpauer, 1864)	0.125	0.0001
<i>Turritopsis nutricula</i> McCrady, 1857	1.000	0.0008
<i>Zanclaea</i> sp.	0.125	0.0001
<i>Zyzyzus warreni</i> Calder, 1988	0.250	0.0009
Campanulinidae indet.1 *		
<i>Cladocoryne floccosa</i> Rotch, 1871 *		

* species found only in annual samples.

Seasonality and microhabitat

Cnidarian assemblages were different in all 8 periods (Pseudo-F = 5.7429; P(perm) = 0.0001) and on inner and outer surfaces (Pseudo-F = 4.1181; P(perm) = 0.0001). Period of submersion and surface occupied interacted (Pseudo-F = 1.2268; P(perm) = 0.0472). The first year assemblages were different from those of the second year (Pseudo-F = 2.1967; P(perm) = 0.0059). Most pairwise comparisons revealed differences between periods, and for samples of the same period in different years only November was similar in both years (Table 2). Differences were not due to different dispersions (Table 3).

Table 2. PERMANOVA pairwise tests for the structure of the assemblages of cnidarians among the eight 3-month periods for outer and inner surfaces at Ilhabela (Brazil). Significant differences are marked in grey.

Retrieval periods	Outer		Inner	
	t	P(perm)	t	P(perm)
May 10, August 10	2.54	0.001	1.76	0.001
May 10, November 10	2.62	0.001	2.10	0.001
May 10, February 11	2.47	0.001	1.83	0.001
May 10, May 11	1.81	0.001	1.49	0.007
May 10, August 11	2.28	0.001	1.78	0.001
May 10, November 11	2.02	0.001	2.13	0.001
May 10, February 12	2.19	0.001	1.97	0.001
August 10, November 10	1.85	0.001	1.63	0.008
August 10, February 11	2.34	0.001	1.76	0.001
August 10, May 11	2.20	0.001	1.62	0.001
August 10, August 11	1.51	0.013	1.46	0.003
August 10, November 11	1.91	0.001	2.18	0.001
August 10, February 12	1.57	0.007	1.69	0.001
November 10, February 11	2.27	0.001	1.53	0.018
November 10, May 11	2.41	0.001	2.24	0.001
November 10, August 11	1.04	0.357	1.27	0.083
November 10, November 11	1.57	0.005	1.24	0.120
November 10, February 12	1.49	0.005	1.31	0.079
February 11, May 11	1.58	0.002	1.55	0.008
February 11, August 11	2.19	0.001	1.88	0.001
February 11, November 11	1.99	0.001	1.72	0.001
February 11, February 12	1.98	0.001	1.73	0.001
May 11, August 11	2.13	0.001	1.98	0.001
May 11, November 11	2.13	0.001	2.47	0.001
May 11, February 12	2.01	0.001	2.23	0.001
August 11, November 11	1.16	0.167	1.65	0.001
August 11, February 12	1.12	0.207	1.25	0.085
November 11, February 12	1.44	0.010	1.44	0.019

Table 3. Comparison in dispersion between outer and inner surfaces showing that they are similar (PERMDISP pairwise tests) during the eight 3-mo periods at Ilhabela (Brazil).

Retrieval periods	Outer		Inner	
	t	P(perm)	T	P(perm)
May 10, August 10	0.10	0.930	0.23	0.844
May 10, November 10	0.66	0.587	0.45	0.676
May 10, February 11	0.69	0.547	1.07	0.326
May 10, May 11	0.95	0.429	0.61	0.595
May 10, August 11	0.62	0.610	0.02	0.987
May 10, November 11	1.58	0.219	0.13	0.908
May 10, February 12	1.17	0.336	0.63	0.578
August 10, November 10	0.74	0.531	0.18	0.869
August 10, February 11	0.77	0.494	0.75	0.485
August 10, May 11	1.03	0.375	0.84	0.460
August 10, August 11	0.71	0.539	0.24	0.828
August 10, November 11	1.62	0.175	0.36	0.757
August 10, February 12	1.23	0.277	0.86	0.448
November 10, February 11	0.01	0.999	0.69	0.482
November 10, May 11	0.19	0.863	1.17	0.264
November 10, August 11	0.09	0.935	0.49	0.640
November 10, November 11	1.02	0.384	0.60	0.562
November 10, February 12	0.48	0.662	1.21	0.263
February 11, May 11	0.20	0.842	1.93	0.067
February 11, August 11	0.10	0.929	1.22	0.234
February 11, November 11	1.07	0.343	1.24	0.239
February 11, February 12	0.52	0.612	1.98	0.058
May 11, August 11	0.33	0.752	0.69	0.520
May 11, November 11	1.08	0.351	0.48	0.650
May 11, February 12	0.43	0.674	0.01	0.990
August 11, November 11	1.18	0.308	0.16	0.889
August 11, February 12	0.65	0.561	0.72	0.507
November 11, February 12	0.70	0.554	0.50	0.647

Samples overlapped in all periods, even though most periods are still different (Figure 8a-b). Centroids for periods of outer surfaces have five points relatively close together (Figure 8c) while centroids are more dispersed for inner surfaces (Figure 8d). Ignoring surface, centroids of all periods are relatively distant from each other (Figure 8e) and the assemblages of cnidarian from equivalent periods in different years are different.

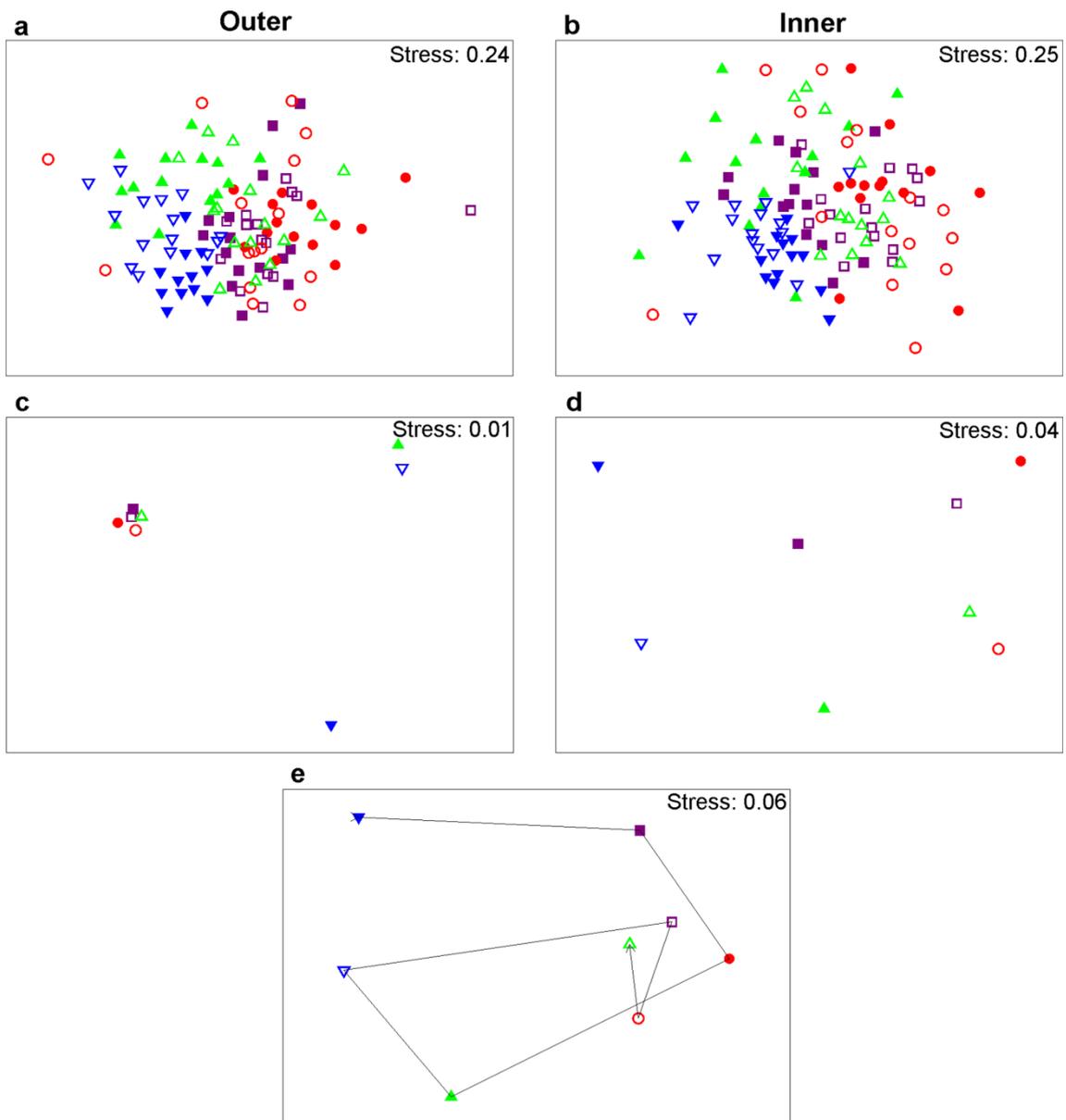


Figure 8. nMDS plots (a, b) and distances among the centroids of the periods (c, d, e) showing differences in the assemblages of cnidarians among the 8 periods for outer (a, c), inner (b, d) and all surfaces (e) at Ilhabela (Brazil), from February 2010 to February 2012. Solid symbols = first year; hollow symbols = second year. Blue triangle = May; purple square = August; red circle = November; green triangle = February. The line in (e) connects subsequent periods chronologically.

A subset of 13 species (45%) on outer surfaces explains the nMDS patterns with a correlation of $r = 0.953$, while 12 species (40%) on inner surfaces explains the pattern with a correlation of $r = 0.955$ (Table 4). Most of these species explaining the nMDS patterns were the same for outer and inner surfaces.

Table 4. Results from BVSTEP showing the smallest subset of species that generated temporal patterns in nMDS for the outer and inner samples at Ilhabela (Brazil). Species in bold were in the subset of only one surface.

Outer	Inner
<i>Acharadria crocea</i>	<i>Acharadria crocea</i>
<i>Bimeria vestita</i>	<i>Bougainvillia muscus</i>
<i>Bougainvillia muscus</i>	<i>Clytia cf. gracilis</i>
<i>Clytia cf. gracilis</i>	<i>Clytia linearis</i>
<i>Eudendrium caraiuru</i>	<i>Eudendrium caraiuru</i>
<i>Filellum sp.</i>	<i>Filellum sp.</i>
<i>Halecium bermudense</i>	<i>Halecium bermudense</i>
<i>Halecium tenellum</i>	<i>Halopteris alternate</i>
<i>Halopteris alternate</i>	<i>Lafoeina amirantensis</i>
<i>Lafoeina amirantensis</i>	<i>Obelia bidentata</i>
<i>Obelia bidentata</i>	<i>Obelia dichotoma</i>
<i>Obelia dichotoma</i>	<i>Turritopsis nutricula</i>
<i>Turritopsis nutricula</i>	

Cnidarians were not equally distributed over the surfaces with 67% of total coverage on the outer surface and 33% on the inner surface. Six species were associated with outer surfaces (Table 5) while no species tended to be more associated with the inner surface. Three rare species were exclusive to outer, and five exclusive to inner surfaces (Table 6).

Table 5. Species associated with outer surfaces found with the point-biserial correlation coefficient test in eight 3-month periods at Ilhabela (Brazil), from February 2010 to February 2012. There was no significant association with the inner surface.

Species	Stat.	p-value
<i>Acharadria crocea</i>	0.161	0.004
<i>Eudendrium caraiuru</i>	0.139	0.032
<i>Halecium bermudense</i>	0.170	0.008
<i>Lafoeina amirantensis</i>	0.154	0.026
<i>Obelia dichotoma</i>	0.256	0.001
<i>Obelia bidentata</i>	0.234	0.001

Table 6. Species that were exclusively on either the outer and inner surfaces for the eight 3 - month periods at Ilhabela (Brazil), from February 2010 to February 2012.

Outer	Inner
Haleciidae indet.2	<i>Clytia cf. stolonifera</i>
<i>Monothecca margaretta</i>	Haleciidae indet.1
Pandeidae indet.1	<i>Parawrightia robusta</i>
	<i>Sertularia marginata</i>
	<i>Zanclaea sp.</i>

Biotic interactions

Epibiosis and resistance to overgrowth varied among the species. A total of 34% epibionts were found in the 3-month samples (Annex II), and 29% were found resisting overgrowth by tunicates, bryozoans, sponges and even hydrozoans (Annex III).

Annual samples

Two additional taxa were found on the annual samples for a total of 36 species. The number of species recorded for each year of the annual samples was usually greater than that during the 3-month periods (Figure 9). But, combining 3 mo samples for each year resulted in greater richness than the yearly samples (Figure 10).

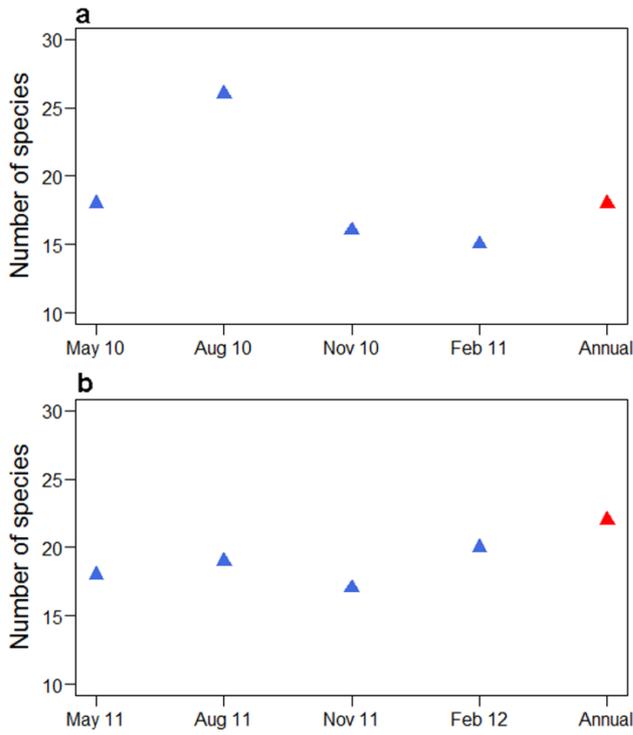


Figure 9. Species richness found in each 3-month (blue) and annual (red) periods for the first (a) and the second (b) year at Ilhabela (Brazil).

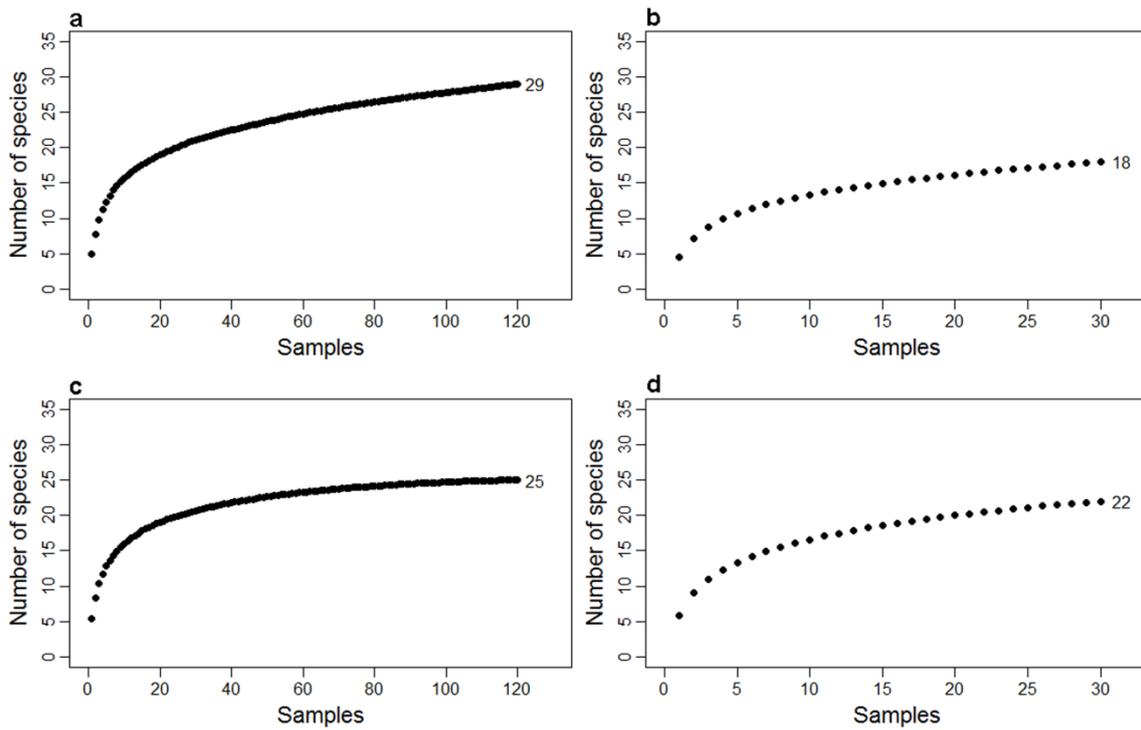


Figure 10. Sample-based rarefaction curves for the first year of 3-month (a) and annual (b) samples, and second year of 3-month (c), annual (d) samples at Ilhabela (Brazil), from February 2010 to February 2012.

All 3 mo and annual samples varied in their cnidarian assemblages (PERMANOVA, Pseudo-F = 5.2319; P(perm) = 0.0001) as did inner and outer surfaces (Pseudo-F = 4.2315; P(perm) = 0.0002). Time and Surface did not interact (Pseudo-F = 1.1459; P(perm) = 0.1112). Three month samples taken together were different from the annual samples (Pseudo-F = 4.3314; P(perm) = 0.0001), and also each year separately (first year Pseudo-F = 3.4703; P(perm) = 0.0006; second year Pseudo-F = 2.2782; P(perm) = 0.0032). Some differences may have been a consequence of different dispersions (Table 7).

Annual samples overlap with all 3 mo samples (Figure 11a), but centroids of annual samples are closer to the respective 3 mo samples retrieved at the same moment than to any other 3 mo sample (Figure 11b).

Table 7. Pairwise tests (PERMANOVA) for the structure of the assemblages of cnidarians and pairwise tests (PERMDISP) to compare dispersion among all 10 sets of samples (eight 3-month and two annual) at Ilhabela (Brazil). Statistically significant differences are marked in grey.

Retrieval Periods	PERMANOVA		PERMDISP	
	t	P(perm)	t	P(perm)
May 10, August 10	2.86	0.001	0.17	0.882
May 10, November 10	3.16	0.001	0.59	0.619
May 10, February 11	2.72	0.001	0.99	0.365
May 10, May 11	2.11	0.001	0.33	0.772
May 10, August 11	2.76	0.001	0.12	0.921
May 10, November 11	2.60	0.001	2.25	0.040
May 10, February 12	2.73	0.001	0.18	0.871
May 10, Annual 11	2.77	0.001	1.38	0.221
May 10, Annual 12	2.10	0.001	1.70	0.146
August 10, November 10	2.22	0.001	0.38	0.742
August 10, February 11	2.66	0.001	0.72	0.502
August 10, May 11	2.64	0.001	0.49	0.653
August 10, August 11	1.93	0.001	0.29	0.801
August 10, November 11	2.54	0.001	1.87	0.085
August 10, February 12	1.86	0.001	0.01	0.995
August 10, Annual 11	2.28	0.001	1.08	0.328
August 10, Annual 12	1.68	0.001	1.40	0.216
November 10, February 11	2.56	0.001	0.35	0.753
November 10, May 11	3.23	0.001	0.99	0.356
November 10, August 11	1.46	0.018	0.75	0.510
November 10, November 11	1.67	0.003	1.64	0.125

November 10, February 12	1.84	0.001	0.43	0.704
November 10, Annual 11	2.31	0.001	0.75	0.503
November 10, Annual 12	2.03	0.001	1.12	0.326
February 11, May 11	2.14	0.001	1.51	0.145
February 11, August 11	2.70	0.001	1.21	0.254
February 11, November 11	2.19	0.001	1.53	0.140
February 11, February 12	2.32	0.001	0.84	0.428
February 11, Annual 11	1.41	0.025	0.47	0.654
February 11, Annual 12	1.87	0.001	0.91	0.394
May 11, August 11	2.87	0.001	0.22	0.829
May 11, November 11	3.03	0.001	3.00	0.004
May 11, February 12	2.84	0.001	0.55	0.610
May 11, Annual 11	2.50	0.001	1.96	0.064
May 11, Annual 12	2.27	0.001	2.25	0.038
August 11, November 11	1.72	0.001	2.60	0.013
August 11, February 12	1.36	0.023	0.32	0.779
August 11, Annual 11	2.44	0.001	1.63	0.126
August 11, Annual 12	1.71	0.001	1.94	0.078
November 11, February 12	1.73	0.001	2.19	0.042
November 11, Annual 11	2.25	0.001	1.06	0.308
November 11, Annual 12	1.84	0.001	0.43	0.691
February 12, Annual 11	2.01	0.001	1.26	0.245
February 12, Annual 12	1.54	0.005	1.59	0.145
Annual 11, Annual 12	1.32	0.047	0.50	0.639

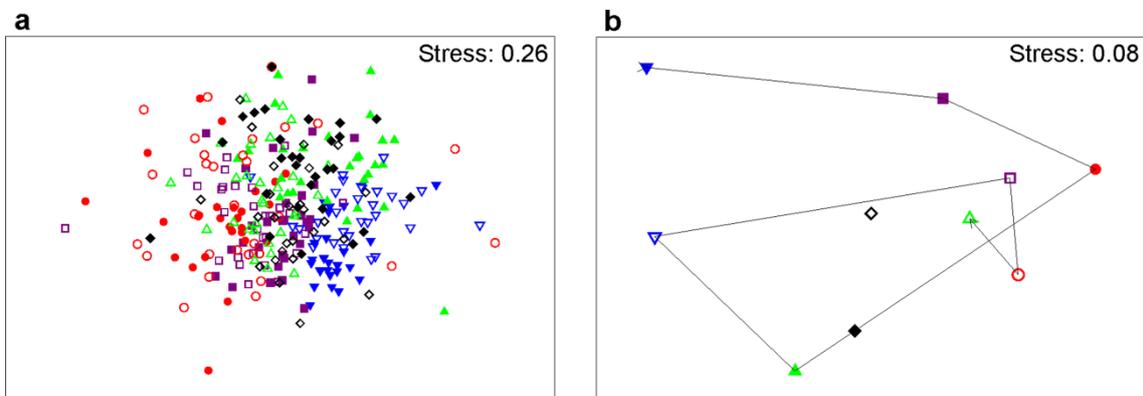


Figure 11. nMDS plot (a) and distances among each centroid of the periods (b) showing differences in the assemblages of the cnidarians among the eight 3-month periods and the two annual periods at Ilhabela (Brazil), from February 2010 to February 2012. Solid symbols = first year; hollow symbols = second year. Blue triangle = May; purple square = August; red circle = November; green triangle = February; black diamond = 1-year sample. The line in (b) connects sequential points in time, except by the two annual points.

DISCUSSION

Cnidarian assemblages are clearly variable throughout the year and among years. Variations in composition are probably a consequence of temperature seasonality, the greatest species turnover following a period of extremely variable sea surface temperature. However, structure of the benthic cnidarian assemblages in terms of both, composition and abundance, was not clearly seasonal, but rather variation in assemblage structure occurred during essentially all consecutive periods. Also, assemblage structure was quite different from year to year.

Inner and outer surface assemblages also varied. Such variation is probably due to a combination of different settling patterns, different mortality patterns and different predation pressures (Keough & Downes, 1982). Nonetheless, species explaining the temporal patterns in the nMDS were essentially the same for both surfaces. Cover was also different between the surfaces, and that may have been due to differential water flow over the surfaces due to different hydrodynamics. This may have resulted in reduced feeding rates for suspension feeders on inner surfaces (Gili & Hughes, 1995).

Obelia dichotoma was the only core species, very abundant and common over time. This species is very competitive as an epibiont on other invertebrates (30% of the records) that also resists being overgrown (43% of the records) by other organisms. The satellite *Turritopsis nutricula* was frequent in time but not abundant. It was found to be restricted to certain time periods in the SSC, inferred from its presence on 1-2 month test panels (Migotto *et al.*, 2001). Therefore, *T. nutricula* seems to be changing its local abundance over time, as predicted by the core-satellite model (Hanski, 1982).

The temporal bimodal pattern for species distributions, in which most species were either present in all periods or in only one, is surprising. While the core-satellite model was first proposed to explain space occupation (Hanski, 1982), our data suggest that it may also apply to occupation over time (Magurran, 2007). In addition, the spatial pattern observed here is not bimodal and many species are rare (along a gradient between rare and satellite) and very few are extremely abundant (one core, in this case). The combined temporal and spatial

distributions resulted in a triangular pattern, in which rare species are found in a variety of temporal frequencies, but abundant species are necessarily found throughout the year.

Epizoism was frequent in the 3 mo samples, in contrast with patterns found in 1994-1995 in a study of recruitment on 1 and 2-month test panels in the SSC (Migotto *et al.*, 2001). An explanation for this difference in results may be that competition for space increases over time because of colony growth, and this may take longer than two months for its effects to be seen. There was also relative high survival of species to overgrowth, suggesting important interactions in these assemblages and that many species may have already died after 3 months. For example, some samples were completely covered by the tunicate *Didemnum perlucidum*, clearly reducing survival of those species that were overgrown. These patterns highlight the importance of biotic interactions, such as competition, and their role in assemblage structure.

Change in species composition of fouling communities is constant (Sutherland & Karlson, 1977), what may have caused the similar patterns found for the 3-month and annual samples retrieved in February 2011 and in February 2012. This supports the hypothesis that subtropical fouling assemblages are not directional, but rather simply keep changing (Sutherland & Karlson, 1977). Because the greatest richness was usually in annual samples, this suggests that the number of species after 3 mo is still increasing. This pattern in hydroids, the vast majority of cnidarians in our samples, should be tested in other taxa.

In conclusion, cnidarians assemblages can be structured by microhabitat, biotic interactions and time of submersion. Assemblages vary temporally in species compositions, but abundance is not seasonally determined. These dynamics, and consequent variation in recruitment, are the results of many factors which will have to be considered when attempting to manage fouling communities.

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ANNEXES

Annex I. Submersion and retrieval dates of 3-month and annual test panels at Ilhabela (Brazil).

Time interval	Submersion	Retrieval
3-month	10 February 2010	3 May 2010
	3 May 2010	4 August 2010
	4 August 2010	4 November 2010
	4 November 2010	3 February 2011
	3 February 2011	3 May 2011
	3 May 2011	3 August 2011
	3 August 2011	3 November 2011
	3 November 2011	2 February 2012
Annual	10 February 2010	3 February 2011
	3 February 2011	2 February 2012

Annex II. Species recorded for 3-month panels and their occurrence as epibionts on other organisms or directly on panel surface. The two right columns show the relative frequencies. Panels were placed at Ilhabela (Brazil). Ant = Anthozoa; Asc = Ascidiacea; Biv = Bivalvia; Bry = Bryozoa; Cirr = Cirripedia; Hyd = Hydrozoa; Pol = Polychaeta; Por = Porifera; Alg = Filamentous algae.

	Ant	Asc	Biv	Bry	Cirr	Hyd	Pol	Por	Alg	Total Epibionts	On panels	Epibionts frequency	Frequency on panels
<i>Acharadria crocea</i>	0	5	0	50	5	6	0	0	0	66	944	0.07	0.93
<i>Actinaria indet.7</i>	0	4	1	8	0	0	0	0	0	13	23	0.36	0.64
<i>Actinaria indet.8</i>	0	13	0	6	0	0	0	0	0	19	18	0.51	0.49
<i>Bimeria vestita</i>	0	0	0	41	0	7	0	0	0	48	38	0.56	0.44
<i>Bougainvillia muscus</i>	0	35	1	126	8	28	12	2	0	212	734	0.22	0.78
<i>Clytia cf. gracilis</i>	0	10	0	136	0	23	7	8	0	184	456	0.29	0.71
<i>Clytia linearis</i>	0	60	2	178	1	25	8	8	0	282	545	0.34	0.66
<i>Clytia cf. stolonifera</i>	0	1	0	0	0	0	0	0	0	1	4	0.20	0.80
<i>Corydendrium parasiticum</i>	0	0	3	1	0	0	0	0	0	4	282	0.01	0.99
<i>Coryne sp.</i>	0	10	0	36	0	0	0	1	0	47	24	0.66	0.34
<i>Diphasia digitalis</i>	0	0	0	3	0	0	0	0	0	3	4	0.43	0.57
<i>Eudendrium caraiuru</i>	0	7	0	76	0	1	1	1	0	86	617	0.12	0.88
<i>Eudendrium carneum</i>	0	0	0	10	0	0	0	0	0	10	36	0.22	0.78
<i>Filellum sp.</i>	0	0	0	15	0	4	6	0	0	25	113	0.18	0.82
Haleciidae indet.1	0	0	0	0	0	0	0	0	0	0	7	0.00	1.00
Haleciidae indet.2	0	0	0	0	0	0	0	0	0	0	3	0.00	1.00
<i>Halecium bermudense</i>	0	226	1	129	1	11	6	94	0	468	1032	0.31	0.69
<i>Halecium dyssymetrum</i>	0	0	0	1	0	0	0	0	0	1	2	0.33	0.67
<i>Halecium tenellum</i>	0	1	2	30	0	8	0	0	0	41	66	0.38	0.62
<i>Halopteris alternata</i>	1	139	5	214	1	9	12	65	1	447	963	0.32	0.68
<i>Lafoea sp.</i>	0	1	0	2	0	0	0	0	0	3	2	0.60	0.40
<i>Lafoeina amirantensis</i>	0	8	0	393	0	128	7	0	1	537	14	0.97	0.03
<i>Monotheca margareta</i>	0	0	0	0	0	0	0	0	0	0	1	0.00	1.00
<i>Obelia bidentata</i>	0	48	0	692	1	95	4	1	4	845	160	0.84	0.16
<i>Obelia dichotoma</i>	0	103	2	903	2	64	7	3	4	1088	2401	0.31	0.69
Pandeidae indet.1	0	0	0	0	0	0	0	0	0	0	1	0.00	1.00
<i>Parawrightia robusta</i>	0	0	0	0	0	0	0	0	0	0	3	0.00	1.00
<i>Pennaria disticha</i>	0	0	0	5	1	0	0	0	0	6	112	0.05	0.95
<i>Plumularia cf. strictocarpa</i>	0	0	0	0	0	0	0	0	0	0	6	0.00	1.00
<i>Sertularella tenella</i>	0	12	0	11	0	2	1	0	0	26	125	0.17	0.83
<i>Sertularia marginata</i>	0	0	0	0	0	0	0	0	0	0	2	0.00	1.00
<i>Turritopsis nutricula</i>	0	18	1	10	0	0	0	3	0	32	81	0.28	0.72
<i>Zanclaea sp.</i>	0	0	0	0	0	0	0	0	0	0	1	0.00	1.00
<i>Zyzyzus warreni</i>	0	15	0	5	0	0	0	2	0	22	7	0.76	0.24
TOTAL	1	716	18	3081	20	411	71	188	10	4516	8827	0.34	0.66

Annex III. Species recorded for 3-month panels at Ilhabela (Brazil) and their occurrence resisting to other invertebrates overgrown or growing freely. The two right columns show the relative frequencies. Asc = Ascidiacea; Bry = Bryozoa; Hyd = Hydrozoa; Por = Porifera.

	Asc	Bry	Hyd	Por	Total with overgrowth	Free specimens	Overgrowth frequency	Frequency of free specimens
<i>Acharadria crocea</i>	329	223	0	16	568	442	0.56	0.44
<i>Actinaria indet.7</i>	0	0	0	0	0	36	0.00	1.00
<i>Actinaria indet.8</i>	0	0	0	0	0	37	0.00	1.00
<i>Bimeria vestita</i>	5	4	0	0	9	77	0.10	0.90
<i>Bougainvillia muscus</i>	130	154	0	15	299	647	0.32	0.68
<i>Clytia cf. gracilis</i>	21	26	0	8	55	585	0.09	0.91
<i>Clytia linearis</i>	92	22	0	12	126	701	0.15	0.85
<i>Clytia cf. stolonifera</i>	4	0	0	0	4	1	0.80	0.20
<i>Corydendrium parasiticum</i>	47	17	0	5	69	217	0.24	0.76
<i>Coryne sp.</i>	1	1	0	0	2	69	0.03	0.97
<i>Diphasia digitalis</i>	3	0	0	0	3	4	0.43	0.57
<i>Eudendrium caraiuru</i>	176	100	0	8	284	419	0.40	0.60
<i>Eudendrium carneum</i>	7	9	0	2	18	28	0.39	0.61
<i>Filellum sp.</i>	0	0	0	0	0	138	0.00	1.00
<i>Haleciidae indet.1</i>	0	0	0	0	0	7	0.00	1.00
<i>Haleciidae indet.2</i>	0	0	0	0	0	3	0.00	1.00
<i>Halecium bermudense</i>	203	31	0	44	278	1222	0.19	0.81
<i>Halecium dyssymetrum</i>	0	0	0	0	0	3	0.00	1.00
<i>Halecium tenellum</i>	7	1	0	2	10	97	0.09	0.91
<i>Halopteris alternata</i>	316	26	0	93	435	975	0.31	0.69
<i>Lafoea sp.</i>	0	0	0	0	0	5	0.00	1.00
<i>Lafoeina amirantensis</i>	0	0	0	0	0	551	0.00	1.00
<i>Monotheca margaretta</i>	0	0	0	1	1	0	1.00	0.00
<i>Obelia bidentata</i>	46	23	0	11	80	925	0.08	0.92
<i>Obelia dichotoma</i>	696	700	1	94	1491	1998	0.43	0.57
<i>Pandeidae indet.1</i>	0	0	0	0	0	1	0.00	1.00

<i>Parawrightia robusta</i>	0	1	0	0	1	2	0.33	0.67
<i>Pennaria disticha</i>	30	41	0	0	71	47	0.60	0.40
<i>Plumularia cf. strictocarpa</i>	2	0	0	0	2	4	0.33	0.67
<i>Sertularella tenella</i>	47	2	0	4	53	98	0.35	0.65
<i>Sertularia marginata</i>	0	1	0	0	1	1	0.50	0.50
<i>Turritopsis nutricula</i>	8	6	0	12	26	87	0.23	0.77
<i>Zanclaea sp.</i>	0	0	0	0	0	1	0.00	1.00
<i>Zyzyzus warreni</i>	0	0	0	7	7	22	0.24	0.76
TOTAL	2170	1388	1	334	3893	9450	0.29	0.71

CONSIDERAÇÕES FINAIS

Este estudo revelou diferentes escalas de variação que, em conjunto, permitem um melhor entendimento da forma como assembleias de cnidários bentônicos estão estruturadas, destacando a importância de somar-se uma perspectiva temporal às diferentes escalas espaciais (Magurran, 2007).

A riqueza de espécies é maior no equatorial Pecém, não atingindo igual número em Ilhabela mesmo considerando-se o dobro do tempo de amostragem. Houve variação temporal grande e constante na composição de espécies da assembleia equatorial de cnidários bentônicos em oposição à variação que acompanha sazonalidade da temperatura na assembleia tropical-subtropical. Porém, há ausência de definição sazonal quando a composição e a abundância são consideradas em conjunto ao longo de dois anos em Ilhabela. Esta incongruência entre os anos mostra que, apesar de comunidades marinhas variarem temporalmente de forma diferente em diferentes latitudes, variações relacionadas à composição e à abundância são imprevisíveis.

Padrões gerais de variação temporal emergiram da comparação entre os locais, uma vez que, apesar da existência de variação local na composição de espécies ao longo de dois anos em Ilhabela, as assembleias não chegam a se estruturar temporalmente de forma semelhante à do Pecém, o que mostra que as diferenças entre regiões superam a variação local.

Claramente, diferentes espécies possuem diferentes papéis nessa estrutura. Algumas espécies mais abundantes são responsáveis por predizer padrões sazonais. No entanto, espécies mais raras, menos importantes na estruturação sazonal, são importantes na estruturação de um padrão bimodal de ocorrência temporal, com espécies sempre presentes e espécies raramente presentes, observado tanto para Ilhabela quanto para o Pecém. Este padrão evidencia que a disposição da diversidade não é somente espacial, mas também temporal (White *et al.*, 2006), e destaca a importância das espécies raras nessa estruturação, colocando estes fatores como importantes em estratégias que busquem acessar e até mesmo preservar a biodiversidade.

O frequente sobrecrescimento e epizoísmo de espécies sugerem interações importantes no canal de São Sebastião, que tendem a ser ainda mais intensas no Pecém

(Freestone & Osman, 2011; Freestone *et al.*, 2011) e que causam imprevisibilidade de colonização das placas.

Concluimos que fatores agindo em escala latitudinal, como a variação climática e a riqueza de espécies, assim como em escala local, como microhabitats e interações bióticas, são importantes na estruturação de assembleias de cnidários bentônicos e devem ser levados em consideração quando se busca entender padrões em comunidades marinhas, inclusive para fins de conservação. Destacamos a importância da perspectiva temporal e, ainda, como ambientes cada vez mais impactados pela ação humana dificultam a interpretação e a previsão de padrões.

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RESUMO

Diferentes escalas espaciais, nas quais diferentes fatores variam, podem ser importantes em estudos da biodiversidade. Estrutura e dinâmica de comunidades marinhas epifaunais variam com a latitude, mas como essa variação muda ao longo do tempo é pouco estudada. Investigamos como a estrutura de assembleias de cnidários bentônicos em portos varia temporalmente em uma latitude tropical e uma subtropical e devido a fatores locais. No Brasil, estudamos recrutamento ao longo de quatro trimestres em duas áreas portuárias (Pecém a 3°32'S e Ilhabela a 23°46'S), e ao longo de dois anos em Ilhabela. Verificamos que (1) a riqueza de espécies segue o gradiente latitudinal, com assembleias de cnidários bentônicos mais ricas no Pecém, o local mais tropical; (2) a composição das assembleias varia muito ao longo do tempo, mas é mais constante na latitude tropical e parece ser uma consequência de maior variação sazonal da temperatura na latitude subtropical; (3) as abundâncias dos membros das assembleias de Ilhabela não são sazonalmente definidas; (4) cada local possui diferentes táxons que são mais importantes na estrutura da assembleia; (5) as assembleias em Ilhabela estão estruturadas conforme o microhabitat, interações bióticas e tempo de submersão. Este estudo destaca a importância da perspectiva temporal no entendimento da dinâmica de comunidades, contribui com o entendimento da importância da escala na determinação de padrões em comunidades marinhas e de como impactos humanos no ambiente dificultam a interpretação e previsão de padrões em comunidades.

ABSTRACT

A variety of spatial scales, in which different factors vary, can be important in studies of biodiversity. Structure and dynamics of marine epifaunal communities are known to vary latitudinally, but how that variation changes over time is relatively unstudied. Here we investigate how the structure of fouling assemblages of cnidarians in harbors varies temporally at a tropical and a subtropical latitude and due to local factors. In Brazil, we studied recruitment during four 3 month periods in two harbors (tropical Pecém at 3°32'S and subtropical Ilhabela at 23°46'S) and over two years at Ilhabela. We found that (1) species richness follows a latitudinal gradient with more speciose benthic cnidarian assemblages at tropical Pecém; (2) composition of the assemblages varies widely over time, while being more constant at the tropical latitude and seems to be a consequence of greater seasonal variation in temperature at the subtropical latitude; (3) abundance of members of the assemblages at Ilhabela are not seasonally defined; (4) each site has different taxa that are more important in assemblage structure; (5) assemblages at Ilhabela are structured by microhabitat, biotic interactions and time of submersion. This study highlights the importance of a temporal perspective in understanding community dynamics, contributes to the understanding of the importance of scale in determining patterns of marine communities and how human impacts difficult interpretation and prediction of community patterns.