Beta diversity in rocky subtidal macroalgal assemblages from Bahía de Loreto, Gulf of California, Mexico

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Abstract

We evaluated the contribution of beta (β) diversity of macroalgal assemblages in subtropical rocky reefs of the Gulf of California. Seasonal samplings of macroalgae were taken in six sites from 2005 to 2008. We identified 157 species, with a local richness [alpha (α) diversity] between 8 and 38 species, with the lowest values in fall. Additive partitioning of species diversity show that β diversity contributed between 61% and 70% of gamma diversity, without differences among seasons. The temporal β diversity (measured as the qualitative dissimilarity between consecutive seasons of the year) was between 49% and 94% dissimilarity, with higher values in the seasonal transition from fall to winter. Increased macroalgal mortality by severe environmental conditions during middle summer are probably the most important driver of seasonal variability in α diversity, whereas high levels of β diversity are probably maintained through environmental and biotic variability in space and time and the stochastic processes of mortality and settlement of species. These findings indicate that β diversity is a key diversity component of macroalgal assemblages in subtropical rocky reefs in the Gulf of California.

Keywords: alpha diversity; gamma diversity; natural protected area; seasonality; temporal turnover.

Introduction

One of the great challenges in contemporary ecology is to elucidate the many spatial and temporal processes that affect patterns of biodiversity. To accomplish the enormous task of understanding biodiversity, it is first necessary to describe it in order to propose and test theories that explain the origin and maintenance of biodiversity, and also for conservation purposes (Underwood et al. 2000).

The most common usage of "biodiversity" is to depict the number of species found in a given area, also known as "species diversity" (Magurran 2004). The latter can be partitioned into alpha (α), beta (β), and gamma (γ) components to characterize different aspects (Whittaker 1972). α diversity is measured as the number of species present in a specific location, transect, or sampling unit in a given time (Magurran 2004). γ diversity represents the number of species present in a geographical area or region, over a longer period of time, and it is usually calculated by pooling the observations from a large number of sites inside the region of interest (Whittaker 1972, Moreno and Halffter 2001). β diversity is the degree of change or replacement in the composition of the species in space or time in the area of interest (Koleff 2005), and represents the bridge between α and γ diversity (Whittaker 1972). For that reason, β diversity is usually measured in an additive fashion as the arithmetic difference between α and γ diversity (Lande 1996). Although the measure proposed by Whittaker (1972) has been widely used, the latter approach expresses α , β , and γ diversities in the same units (number of species), allowing their direct comparison (Lande 1996). Also, β diversity can be measured using similarity coefficients and by comparing the number of unique and shared species between the two assemblages. When similarity is low, β diversity reaches a higher value (Koleff 2005).

Each one of the diversity components is the result of different processes that ultimately drive the total diversity found in a specific place. In broad scales, e.g., thousands of kilometers, regional pools of species richness (γ diversity) are determined by historical, phylogenetic, and broad climate processes. In local scales, e.g., from tens to hundreds of centimeters, biotic interactions play a prominent role in determining species diversity within patches of habitat (α diversity). In the middle of these two extremes, qualitative and quantitative changes in the physical and biological characteristics of the habitat can strongly affect variation in the composition and abundance of species among sites or across time; this is β diversity (Halffter and Moreno 2005, Balata et al. 2007a). High values of β diversity have important implications for ecosystem conservation and management because they mean that the biotic compositions and probably the environmental conditions differ between locations to a high degree, and therefore it can be necessary to implement a bigger or a larger number of protected areas to conserve the majority of species (Koleff 2005).

Macroalgae are of key importance in rocky reef communities and contribute significantly to the biodiversity of coastal systems because they function as primary producers, and they provide and modify resources (both habitat and food) for other organisms (Lüning 1990). Naturally, macroalgal assemblages

are variable (e.g., Underwood and Chapman 1998), making the measure of β diversity particularly important, not only to accomplish a better understanding of the functioning of the ecosystems but also for its conservation and sustainability, because anthropogenic disturbances can affect not only α but also ß diversity of algae (Passy and Blanchet 2007, Piazzi and Balata 2008). B diversity from temperate macroalgal assemblages has been related to the slanting of the substrate (Balata et al. 2007a), sedimentation rate (Balata et al. 2007b), and water depth (Balata and Piazzi 2008), indicating that macroalgal β diversity could be driven by changes in physical variables between locations. By comparing β diversity at multiple spatial scales, Smale et al. (2010) found that the turnover of macroalgal assemblages is greater at small scales (5-100 m apart) than at a regional scale (+10 km apart), probably caused by the difference in habitat heterogeneity and the variability in the density of the canopy formers at small scales. In a recent study, Leaper et al. (2011) found that macroalgal assemblages in temperate rocky reefs showed a large amount of turnover (β diversity), having sea surface temperature, wave exposure, and average oxygen concentration as the major predictors of patterns of community change. To our knowledge, there are no studies of β diversity in tropical or subtropical macroalgal assemblages in the eastern Pacific. Therefore, our aim was to quantify the degree in which β diversity contributes to the total diversity of macroalgae in a subtropical area.

The Gulf of California, a semienclosed marginal sea of the eastern Pacific Ocean, is considered among the top 10 marine biodiversity hotspots in the oceans (Roberts et al. 2002). The Pacific Ocean influences the gulf through its mouth at its southern end and it is in this area, included in the tropical-subtropical transitional zone, where complex atmospheric and oceanographic interactions cause strong intra- and interannual variations of the conditions, which in turn might affect the physical processes and biological communities (Lluch-Cota 2000). A good example of this is how the richness and composition of macroalgal assemblages in the gulf are highly variable in space and time (Lively et al. 1993, Pacheco-Ruíz and Zertuche-González 1996a,b, 2002, Paul-Chávez and Riosmena-Rodríguez 2000, Mateo-Cid et al. 2006). Considering the evidence described above, our working hypothesis was that β diversity will have a relevant contribution to the total diversity of macroalgae in space and time, in the rocky reefs of Bahía de Loreto, a subtropical area in the western Gulf.

Materials and methods

Study area

The study took place at Bahía de Loreto National Park in the central-western Gulf of California (Figure 1). The water temperature in this area has seasonal variations ranging from 17.6° C in winter to 30° C in summer (Medina-López 2006). The organic carbon particle concentration is low in summer and more abundant in fall and winter, fluctuating between 0.8 and 4.4 mg l⁻¹ (Medina-López 2006). Salinity shows



Figure 1 Sampled sites in Bahía de Loreto, Gulf of California, Mexico.

little fluctuation throughout the year, between 34.5 and 35.4 psu, and chlorophyll *a* concentration is high in spring (0.76 mg m⁻³) and low in summer (0.05 mg m⁻³) (Medina-López 2006). The average concentration of phosphates is 2 μ mol l⁻¹, there is a constant high concentration of ammonium (11 μ g-at l⁻¹), and nitrite varies between 0.9 and 0.2 μ g l⁻¹ (Comisión Nacional de Áreas Naturales Protegidas 2000).

Six sites were selected in the park (Figure 1), all characterized by the presence of a rocky substrate, *Sargassum* forest, and scattered coral heads. Cardón and Palma have intermixed rocky and sand substrates in <5 m water depth, whereas Choya, Biznaga, Submarino, and Candelero only present hard bottoms, and reach -12 m depth (Table 1).

We made 15 seasonal samplings at each site (January, April, July, and October, representing winter, spring, summer, and fall, respectively) for 4 consecutive years (2005–2008; n=90). At each visit, with scuba diving, we surveyed an area of 900 m², inside of which we collected all macroalgae and at least five boulders covered by algal turfs. The algal material was collected and preserved according to the methods of Tsuda and Abbot (1985). In the laboratory, specimens were identified to the lowest possible taxonomic level by means of their morphological characteristics and on the basis of more than 15 references, all cited in Pacheco-Ruíz and Zertuche-González (1996a,b, 2002). The current names of species were revised using Algaebase (http://www.algaebase.org/; Guiry and Guiry 2010).

Site	Maximum depth (m)	Substrate
Cardón	3	Medium and small rocks between sand
Choya	8	Medium and big rocks overlapping, forming a continuous rocky substrate with holes and walls with different inclinations
Palma	5	Rock bars forming channels with sand and medium rocks between them
Biznaga	12	Medium and big rocks overlapping, forming a continuous rocky substrate with holes and walls with different inclinations
Submarino	10	
G 11	10	

 Table 1
 Depth and type of substrate of six rocky reefs of Bahía de Loreto, Mexico.

α , β , and γ diversity

Candelero

The additive approximation suggested by Lande (1996) was used to estimate the contribution of α diversity and β diversity to γ diversity among sites. α diversity was defined as the number of species present in one place in a given time (Magurran 2004). To obtain β diversity, we calculated the average α diversity ($\overline{\alpha}$), as the mean number of species found at the six sites surveyed in a given time, and γ diversity as the total number of species found at the six sites on the same sampling date (Lande 1996). β diversity was thus obtained by subtraction ($\beta = \gamma - \overline{\alpha}$).

10

Temporal β diversity

The Sørensen index was chosen to measure the temporal β diversity (β_T) between consecutive sampling periods for each one of the sites, as β_T =1-[2a/(b+c)], where "a" is the number of species found in both times of collection, "b" is the number of species that were only found in time 1, and "c" is the number of species that were found only in time 2 (Magurran 2004). This measure of β diversity expresses the difference in composition between two consecutive samplings in percentage of common species, and takes values from 0% when the assemblages are identical to 100% when they have no taxa in common. Four periods of species turnover were used for the calculations during the 4 years of study: winter-spring, spring-summer, summer-fall, and fall-winter (n=78).

Data analysis

To determine the possible spatial and temporal differences in α diversity, we used a two-way analysis of variance (ANOVA) using the six sites and seasons as factors and based on cumulative information to comply with the required degrees of freedom (Zar 2009). The spatial analysis considered all the samples in each site (n=15) as replicates and the temporal analysis considered all samples in each season as replicates (n=24, except spring where n=18). The existence of seasonal differences in $\overline{\alpha}$, β , and γ diversity was tested by a one-way ANOVA test, using the values obtained at each year as replicates (Zar 2009). β_T diversity values at each seasonal transition were compared with a one-way ANOVA to establish if there were differences in the index between turnover periods, using the values obtained at each temporal transition as

replicates (n=18, except for winter-spring where n=24) (Zar 2009). After the ANOVA, a Tukey test was made to detect the origin of the variation, when significant differences were observed (Zar 2009). The data normality and homoscedasticity were previously assessed with the Kolmogorov-Smirnov and Cochran tests (Zar 2009).

Results

At Bahía de Loreto, a total of 157 species of macroalgae were identified: 23% Chlorophyta, 15% Ochrophyta: Phaeophyceae, and 62% Rhodophyta. The frequency of occurrence of the macroalgae was low as 63% was present from 1 to 10 samples, 28% from 11 to 30 samples, and only 9% was present with frequencies >30 samples (Figure 2).

α diversity

The α diversity was between 8 and 38 species; Cardón, Choya, and Palma had slightly lower values (average±standard error), between 18±2 and 19±1 species, than Biznaga, Submarino, and Candelero, with an α diversity between 21±2 and 23±2 species (Figure 3A). Seasonally, α diversity in the fall (17±1 species) was considerably lower than in summer (24±2 species) and winter (21±2 species), but not in spring (19±1 species) (Figure 3B). The two-way ANOVA proved the existence of significant differences in α diversity per season (F₃₆₆=4.73,



Figure 2 Macroalgae species frequency at Bahía de Loreto, Gulf of California, Mexico.



Figure 3 α diversity of macroalgae by site (A) and by season (B) in rocky reefs of Bahía de Loreto, Gulf of California, Mexico. Sites: A, Cardón; B, Choya; C, Palma; D, Biznaga; E, Submarino; F, Candelero. Error bars are standard error.

p<0.01), with a significant difference between fall and summer. There were no differences among sites ($F_{5.66}$ =1.15, p=0.36) or interaction between factors ($F_{15.66}$ =1.02, p=0.43).

$\overline{\alpha}$, β , and γ diversity

The $\overline{\alpha}$ diversity found was 20±1 species (average±standard error) and γ diversity was 60±2 species; therefore, β diversity was 40±1 species, accounting for 67±1% of the total diversity among sites, with little variability of the contributions of $\overline{\alpha}$ and β to γ diversity over time (Figure 4). The lowest β diversity values were in fall (36±2 species), and the highest in summer (45±1 species) and winter (41±4 species). The $\overline{\alpha}$ and

 γ diversity trend was the same as that of β diversity, with the lowest values in fall and highest in summer and winter (Figure 5). The ANOVA did not found significant differences among season in α diversity (F_{3.11}=2.40, p=0.12), β diversity (F_{3.11}=1.61, p=0.24), and γ diversity (F_{3.11}=2.14, p=0.15).

β_T diversity

The β_T diversity had a mean value (±standard error) of 68±1% dissimilarity, with higher values among the seasonal transitions between fall 2005 and summer 2006, and lower values among the seasonal transitions between winter and fall 2007 (Figure 6). The ANOVA showed significant differences in turnover among seasonal transitions ($F_{3.74}$ =5.90, p<0.01), with the β_T diversity measured in autumn–winter (72±2% dissimilarity) higher than that in summer–fall (65±3% dissimilarity); during winter–spring and spring–summer, there were intermediate values (66±2% and 67±3% dissimilarity).

Discussion

In this study, we measured the β diversity of subtropical macroalgal assemblages in space and time using different procedures, the additive partition of diversity components considering sites, and the qualitative dissimilarity between consecutive seasons of the year, during 4 years. Our study shows that macroalgal assemblages of subtropical rocky reefs has a high β diversity, accounting for 67±1% of the γ diversity among sites, and a temporal turnover (β_T) of 68±1% of dissimilarity between seasons, indicating strong changes in species composition in space and time.

The high values of β and β_{T} diversity could be related to the low frequency of occurrence of the species (Figure 2). This could arise as the result of the small size (<20 cm length) and short life span (<1 year) of most algae in the region, so that different species could be present on macroalgal assemblages depending on the availability of space, propagules, or spores (Sousa 1979, 1980, Gray 2000, Vroom et al. 2005), eventually causing fast turnover (Shmida and Wilson 1985). Several



Figure 4 Contribution of $\overline{\alpha}$ diversity and β diversity to γ diversity of macroalgae in rocky reefs of Bahía de Loreto, Gulf of California, Mexico.

wi, winter; sp, spring; su, summer; fa, fall.



Figure 5 $\overline{\alpha}$, β , and γ diversity of macroalgae assemblages by season in rocky reefs of Bahía de Loreto, Gulf of California, Mexico. Error bars are standard error.



Figure 6 β_T (mean dissimilarity percentage, standard error) between consecutive sampling periods of macroalgae, in rocky reefs of Bahía de Loreto, Gulf of California, Mexico.

wi, winter; sp, spring; su, summer; fa, fall. Error bars are standard error.

species in Loreto appeared in just one season, especially spring or early summer, as reported in other areas of the Gulf of California (e.g., Casas-Valdez et al. 1997, Cruz-Ayala et al. 2001, Mateo-Cid et al. 2006). In Loreto, as found in those studies in the gulf that encompass more than an annual sampling program, the presence of different macroalgal assemblages from one year to another in the same location is common (Lively et al. 1993, Pacheco-Ruíz and Zertuche-González 1996a,b, 2002, Paul-Chávez and Riosmena-Rodríguez 2000), thus contributing to the high values of temporal β diversity measured.

High macroalgal spatial turnover had been also found in algae of the Mediterranean Sea (Balata et al. 2007a,b, Balata and Piazzi 2008) and Australia (Smale et al. 2010, Leaper et al. 2011). On these papers, variations in local environmental variables explained the turnover of macroalgae across space, with spatial heterogeneity, temperature, exposure, depth, and oxygen concentration as key factors that influence community composition and its changes. Temporal patterns of β diversity have not been explicitly studied before for macroalgae; however, it is recognized that assemblages in rocky reefs are temporally variable (e.g., Underwood and Chapman 1998). This is especially remarkable in highly seasonal regions such as New England (Mathieson and Penniman 1986), the Red Sea (Ateweberhan et al. 2006), and the Gulf of California (Lively et al. 1993, Paul-Chávez and Riosmena-Rodríguez 2000, Pacheco-Ruíz and Zertuche-González 2002, Mateo-Cid et al. 2006), areas in which it is possible to find a difference of at least 10°C in water temperature between winter and summer.

Our work was not directed to determine what factors are the most important drivers of β diversity among sites or time. However, it is likely that the macroalgal β diversity in the rocky subtidal reefs of Loreto is maintained because of environmental heterogeneity (in space, time, or food resources) combined with the existing niche differences among species (which define ways to respond to environmental heterogeneity) (Loreau 2000); therefore, due to stochastic processes influencing mortality and settlement, unpredictable combinations of species are present in the macroalgal assemblages in a given site and time as found in temperate macroalgal assemblages (Sousa 1979, 1980, Underwood and Chapman 1998).

Specifically, high levels of β diversity among sites in Bahía de Loreto (Figures 4 and 5) are probably the result of the heterogeneity of the reefs, which vary in terms of the nature of the substrate and the environmental conditions among them, including depth, amount of suspended sediments, direction and strength of currents, distance to the coast, and geographic location (Figure 1; Table 1; Gaitán-Morán and Arizpe-Covarrubias 2007), as found in other regions (Balata et al. 2007a,b, Balata and Piazzi 2008, Smale et al. 2010, Leaper et al. 2011). β_{T} diversity of macroalgal assemblages of Bahía de Loreto could be driven primarily by seasonal differences in temperature because it directly affects growth, reproduction, and mortality of the algae and indirectly influences the level and type of biotic interactions (e.g., grazing pressure) between seasons (Lüning 1990). This scenario is coherent with the recorded sea surface temperature in Bahía de Loreto, where a change of 12°C from winter to summer occurs (4 years average±standard error of 19.30±0.16°C in winter and 28.91±1.17°C in summer). Because higher β_{T} occurs in the seasonal transition from fall to winter, where the greater water temperature change, above 10°C, was observed (Figure 6). However, it is clear that changes in species composition cannot be explained by any single factor. Consequently, seasonal changes in other physical variables may be influencing the patterns of distribution and abundance of macroalgal assemblages by imposing physiological constraints on growth and also mediating the type and foraging activity of consumers (Gaines 1985).

Unlike β diversity, α diversity appears to be of lesser importance in determining the total diversity in Bahía de Loreto because it contributes only $33\pm1\%$ of γ diversity among sites. It is considered that α diversity responds to biological interaction such as predation or competition, and to abiotic fluctuations or disturbances (Whittaker 1972). Biological interaction usually occurs over a small spatial scale (centimeters), and the heterogeneity of the rocky coast must allow the establishment of different mosaics of species inside the sampled area (Loreau 2000). Therefore, the seasonal pattern in α diversity, with the lowest values in fall and highest in winter, spring, and summer (Figure 3), is probably the result of the higher water temperature, above 30°C, recorded during August, and low nutrients levels in the water column (0.18 \pm 0.05 μ mol l⁻¹ NO₂ in fall compared with $1.15\pm0.27 \,\mu$ mol l⁻¹ NO₂ in winter; Garcia et al. 2010). These conditions could prevent the flourishing of many species, causing the low number of species found in fall in relation to the other seasons.

The diversity indexes estimated in Bahía de Loreto support the hypothesis that a fundamental component of the diversity of macroalgae in subtropical rocky reefs is the turnover of species among sites and seasons, suggesting that environmental heterogeneity through space and time is responsible for the bulk of diversity. Future work with the aim to determine the principal factors that drive β in subtropical macroalgal assemblages would ideally incorporate multiple spatial and temporal scales, environmental variables, and a measure of

the effect of herbivores in macroalgal assemblages (e.g., abundance and grazing intensity), to be able to discriminate the relevant scales for the maintenance of diversity and the factors that influence the different components of diversity at each scale.

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