

Species richness and morphological diversity of the Genus *Porites* in the Pacific Ocean

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Abstract. Species richness is a common measure of biodiversity, but offers only a partial view of the assemblages. Morphological diversity is another indicator, and can reflect functional aspects of the system more efficiently than the number of taxa. In this study we compared patterns of richness and morphodiversity in the genus *Porites* in the Pacific Ocean. Distribution data of 52 species were arranged in quadrants of 20° of latitude and longitude, and nine morphological characters were measured for each species. The latter data were processed with a principal components analysis, and the diversity of forms was estimated from the geometric mean of the range of the scores of each component. We found out that richness in this genus is concentrated in southeastern Asia, but morphodiversity is more widely distributed and high values appear indistinctly if species number is high or low. The relationship between richness and morphology in *Porites* followed a logarithmic curve and tend to reach an asymptote, and there were no significant differences in morphodiversity of the hemispheres or between the tropics and subtropics. We suggest that the observed morphospace limitations in *Porites* may indicate saturation in niche availability, or occur because of the existence of phyletic boundaries.

Key words: coral, *Porites*, Pacific Ocean, morphology

Introduction

Biological diversity is a complex property that can be measured using any of many traits, from genetic diversity to landscape variety, as each of them offers a different perspective of the phenomenon (Wilson 1996). The most common organization level at which biodiversity has been quantified is the community, and in this case researchers usually focus on species richness as the concept is easy to grasp by the general public and it is intuitively “natural” (Gaston and Spicer 2004). Studies performed in the last decade show that richness tend to correlate well with other biodiversity predictors, and even between different taxonomic groups (Roberts et al. 2002; Qian and Ricklefs 2008). However, in some cases the richness behaves differently to specific and important indicators; for example is not much related to endemism both in the land and marine realms (Hughes et al. 2002; Orme et al. 2005), and because of that situation some authors have called attention to avoid focusing all efforts to preserve only rich areas (Kareiva and Marvier 2003)

One predictor that seems to correlate well with marine species richness is morphological diversity (Roy et al. 2000). The latter has traditionally been considered as a key tool for paleoecological

reconstruction (Foote 1992), and other studies have demonstrated its application for the better understanding of the ecological functioning in Recent coral reefs (Bellwood et al. 2006), gastropod evolution (Latioalis et al. 2006), and comparison of niche space utilized by gastropods living at different depths (McClain et al. 2004). The good fit between form and function was well received because in turn, morphology can reflect the functional aspects of the marine ecosystems very efficiently (Wainwright 2007) as it recognizes particular traits of each species; thus, species richness could be applied as an efficient proximal indicator of ecological functions performed by a certain taxonomic group.

However, not all papers coincide that richness and morphology follow a common trend. For example, Foote (1993) found no relationship or clear trend between richness and morphological diversity in trilobites, and in recent marine organisms the number of species of strombid snails turns out to be a poor indicator of morphological diversity in the Indo Pacific (Roy et al. 2001), basically because certain areas with low richness had a high morphological diversity. Other examples of this situation are cuttlefishes, in which richness and morphological diversity and disparity are independent (Neige 2003).

Corals have a long history of morphological analyses, especially related to taxonomy and phylogeny (Powers and Rohlf 1972; Hoeksema, 1989; Weil et al. 1994), but recently the focus has shifted to more functional aspects related to metabolism, light gathering and others (Enríquez et al. 2005; Todd 2008; Hogenboom et al. 2008). Considering this change of perspective, the objective of this work was to compare the patterns of species richness and morphological diversity in the coral genus *Porites*, as a way to provide a different view of the biodiversity of the taxon. This genus has 60 species (Carpenter et al., 2008), a worldwide distribution and is one of the most conspicuous in reefs. It is also recognized by its ecological role as reef builder and habitat to many species of invertebrates and fishes (Veron 2000).

Methods

To determine species richness of *Porites*, we used the information of 52 species appeared in Veron (2000), and updated it with records from more recent papers. The data (presence-absence) were arranged in quadrants of 20° of latitude and longitude, which covered the entire Pacific Ocean (N=48), and a distribution matrix was completed from where richness was calculated by simple sum.

The morphological study involved nine characters that were measured in museum specimens or from photographs: maximum and minimum corallite (taken as an ellipse), number of septa, number of pali, depth of calices, width of corallite wall, size of columella, ration between depth of calice, and maximum diameter, and type of colony (massive, encrusting or ramose). All measures were taken with a precision of ± 1 mm, and in a minimum of five corallites or images. The set of measurements was standardized (mean= 0, SD = 1) and processed with a principal component analysis, using a covariance matrix (Bakus 2007). This technique allowed the construction of a multidimensional morphospace (Fig. 1) from where we used the geometric mean of the range of the scores of each component to measure the extent of morphological space occupied (Roy et al., 2000, McClain et al., 2004). The last calculation was performed on the data of present species in each quadrant. Finally, a one way ANOVA test (Zar 1999) was applied to look for differences in morphological diversity between hemispheres (north and south), and latitudes (0° to 20°, and 21° to 40°, independent of the hemisphere)

Results

The Fig. 1 shows the empirical morphospace (axis I and II) calculated for the 52 *Porites* species, and we present sketches of the general morphology at each side of the plot. In specific, the left upper corner has

species with a platy morphology (e.g., *Porites tuberculosa* Veron, 2000, *P. densa* Vaughan, 1918), at the upper right we found the ramose species (*P. rugosa* Fenner and Veron, 2000, *P. flavus* Veron 2000), and at the bottom those with encrusting and columnar colonies like *P. solida* Forskaal 1775 and *P. heronensis* Veron, 1985, respectively.

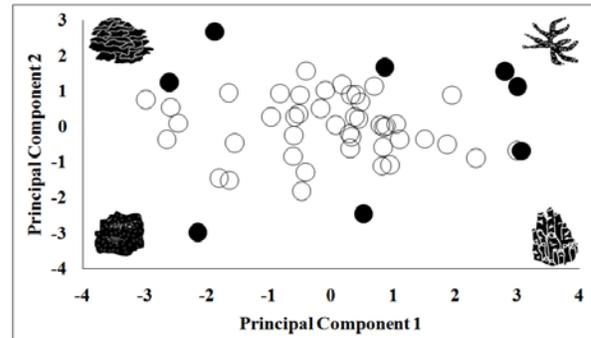


Figure 1. Morphospace of *Porites* in the Pacific Ocean, prepared with principal component analysis.

The map of species richness (Fig. 2) shows that as expected, the highest values can be found at southeastern Asia (over 26 species, and as much as 31), followed by Japan, the Indian Ocean and the Great Barrier Reef (21 to 25). In contrast, the lowest richness occurs in South America, Easter Island and other eastern Polynesian islands, and near the entrance of the Persian Gulf. As it occurs with many marine species, and in particular with corals, there is a clear gradient from the center of marine diversity around Indonesia and Papua New Guinea, to the central and eastern Pacific (Bellwood and Hughes 2001; Roberts et al. 2002).

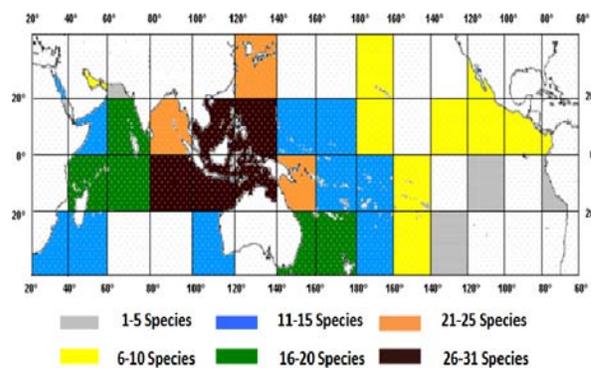


Figure 2. Species Richness of genus *Porites* in the Pacific Ocean.

The situation of morphological diversity was very different (Fig. 3). The index had its highest values in areas including the east coast of Africa, the central Pacific and the equatorial Indian Ocean. It was also

high at the entire north and east coast of Australia and New Caledonia. Interestingly, the areas with lowest morphodiversity (South America and east Polynesia) coincide much more with the results in Fig. 2

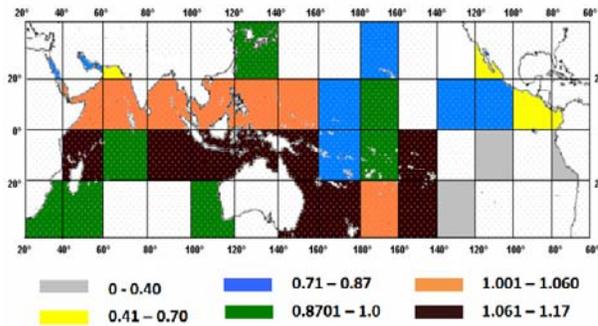


Figure 3. Morphological diversity of the genus *Porites* in the Pacific Ocean.

Comparing species richness and morphological diversity, we can observe that the relationship is not linear, but follows a logarithmic curve. When richness is low (0 to 10 species), the complexity of forms in each quadrat of 20 square degrees rises fast, but in areas where richness is higher than that, the morphodiversity tends to flatten. Also notice that the site where the variety of forms is highest (1.089; eastern Polynesia), there are only seven species present.

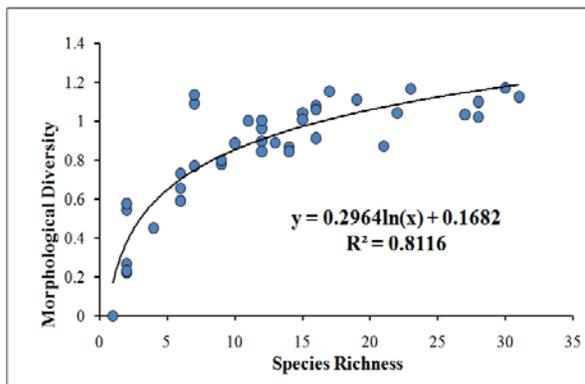


Figure 4. Species richness and morphological diversity in *Porites*. The regression was significant.

To test if sites where richness was higher than 10 can have an effect on morphology, we run a Student *t* test to compare areas with 10 to 20 species with those having 21 or more, and the result indicated no significant differences ($t_{25} = 1.15$, $p > 0.10$). In short, our analyses indicates that morphological diversity in the genus *Porites* do not increases in proportion to

species richness, and that it may exist an upper limit to this biodiversity measure in the Pacific Ocean.

The comparisons between hemispheres (Fig. 4) indicated that richness of *Porites* per site was higher in the Southern Hemisphere than in the Northern ($t_{25} = 3.21$, $p < 0.01$), but that morphodiversity did not differ ($t_{25} = 2.07$, $p > 0.05$). In the case of latitude (Fig. 5), the number of species per site also differed as areas north of 20° N and S were richer ($t_{25} = 5.43$, $p < 0.001$), but as it happened previously, the morphodiversity did not differ between tropical or subtropical zones ($t_{25} = 1.21$, $p > 0.05$).

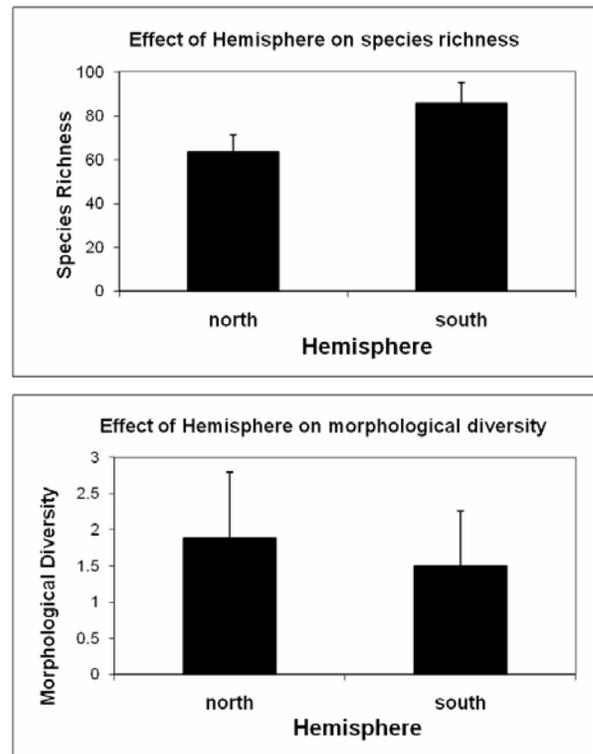


Figure 4. Comparison of richness and morphodiversity of *Porites* between hemispheres in the Pacific Ocean.

Discussion

As shown, morphological diversity and species richness of *Porites* corals behave independently. The scenario that richness generate a variety of forms (and consequently that the relation should be monotonic, or at least positive) has been tested and found in studies of terrestrial animals (Williams and Humphries 1996; Roy and Foote 1997) but nevertheless it does not seem to be the dominant pattern in the marine realm, as it was not found either in gastropods (Roy et al. 2002), sea urchins (González-Azcárraga 2008) or corals (this study). This finding is not necessarily bad news; on the contrary, we propose that the fact that richness and morphodiversity are complementary opens a new

avenue of research in the future, with important ramifications for conservation and functional studies in reef ecosystems.

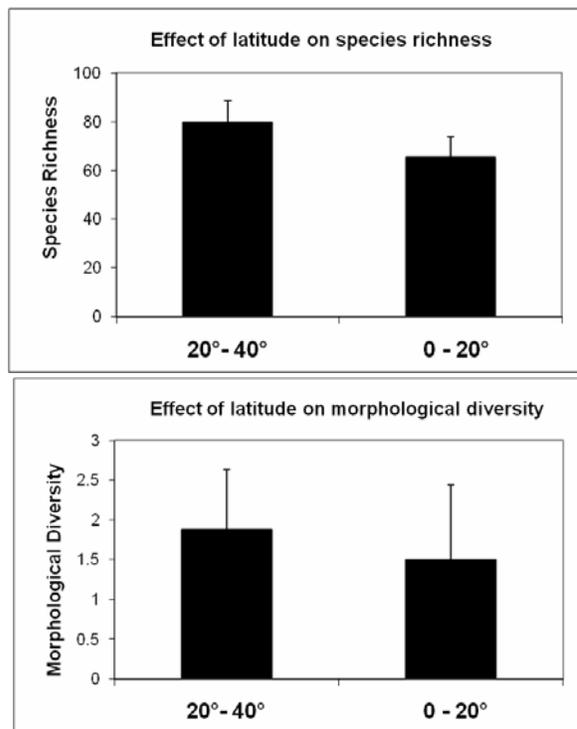


Figure 5. Comparison of richness and morphodiversity of *Porites* between hemispheres in the Pacific Ocean.

In Fig. 3 it is apparent that some regions with few species have remarkably high morphological diversity, including peripheral areas like Polynesia and east Africa. A more in-depth examination should be done, but it is possible that these anomalous areas have at least one endemic species, or a coral with an unusual collection of characters, so the value of the variance in form is increased. However if we consider the Pacific as a unit, morphodiversity in *Porites* is remarkably homogeneous and it seems not to be much influenced by latitude or hemisphere (Figs. 4-5).

Maybe the most important result of the study was the comparison of richness and morphology, which point out that even when both indicators move almost linearly near the axis, the latter eventually tend to reach an asymptote (Fig. 4). This pattern can be explained either from the evolutionary or ecological perspective. In the first one, the genus *Porites* might actually have a phyletic limit in its variety of forms and design (its bauplan), and thus it should be independent of richness. If this idea is correct, a study on fossil species may found that the genus has been transforming in time, and becoming more complex in its calicular and colonial structure. On the other hand,

the limitation in morphology may result if the environment is providing only a limited kind or amount of resources, so that eventually result in saturation of niche availability. There have been many discussions on the size of the niche of hermatypic corals, and of the factors that determine it (Connell 1978; Knowlton and Jackson 1994; Iglesias-Prieto et al. 2004), but the authors coincide that as scleractinians are specialists, its ecological space should be restricted. This observation could explain our results, but there still are many questions to be addressed before obtaining a firm conclusion. Whatever the case, the use of morphological diversity as an indicator of biodiversity of reef corals show promise and should be pursued in future research.

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