Limited potential of deep reefs to serve as refuges for tropical Southwestern Atlantic corals

JULIANO MORAIS1 AND BRÁULIO A. SANTOS2,

1Programa de Pós-Graduação em Ciências Biológicas, Cidade Universitária, Universidade Federal da Paraíba, CEP: 58051-900 João Pessoa, PB, Brazil
2Centro de Ciências Exatas e da Natureza, Departamento de Sistematización e Ecologia, Ciência Universitária, Universidade Federal da Paraíba, CEP: 58051-900 João Pessoa, PB, Brazil

Citation: Morais, J., and B. A. Santos. 2018. Limited potential of deep reefs to serve as refuges for tropical Southwestern Atlantic corals. Ecosphere 9(7):e02281. 10.1002/ecs2.2281

Abstract. The deep reef refuge hypothesis (DRRH) predicts that deep coral reefs may act as refuges against major disturbances affecting shallow reefs, but to date, a few studies have explicitly examined its validity at the community level. We sampled 19 Brazilian reefs distributed between 3 and 61 m depth and tested five DRRH predictions regarding species diversity, distribution, and functional profile of communities. The first prediction was that deep reefs (>30 m depth) should host greater gamma diversity to be able to export species to shallow reefs (<30 m). Second, depth-generalist species should dominate the shallow reefs; otherwise, local extirpation in shallow areas could not be reverted by the deep reefs. Third, alpha diversity should be greater in deep reefs due to reduced anthropogenic pressure in deeper areas. Fourth, beta diversity should be smaller among shallow than deep reefs due to the human-induced spread of a few disturbance-adapted species near sea surface. Finally, the functional composition of shallow reefs should be a subset from that of deep reefs to allow functional recovering of shallower areas. Contrary to expectations, coral communities presented twice more gamma diversity in shallow than deep reefs (13 vs. seven effective species) and only three out of 17 species occurred along the entire gradient. Additionally, the alpha diversity of rare, typical, and dominant species was similar between shallow and deep reefs, and the beta diversity of rare and typical species was about 50% greater in shallow than deep reefs. Supporting the DRRH, coral communities of both reefs were dominated by reef-building, zooxanthellated, gonoehoric corals with brooding or broadcast reproductive mode (Siderastrea stellata and Montastraea cavernosa). However, soft corals were observed only in shallow reefs and azooxanthellated corals were recorded only in deep reefs. These findings revealed a limited potential of deep reefs to serve as refuges for Southwestern Atlantic coral communities, though they may work for two depth-generalist dominant species. We strongly recommend preventing human disturbances at any depth and including both shallow and deep reefs in regional conservation actions.

Key words: Cnidaria; cross-shelf; environmental gradient; Hill numbers; mesophotic coral ecosystems; metacommunity.

Received 23 April 2018; accepted 2 May 2018. Corresponding Editor: Debra P. C. Peters.

Copyright: © 2018 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† E-mail: braulio@dse.ufpb.br

INTRODUCTION

The deep reef refuge hypothesis (DRRH), formerly influenced by Glynn (1996) and coined by Bongaerts et al. (2010), predicts that deep reefs may act as refuge against major disturbances affecting shallow reefs. It stipulates that deep reefs (>30 m depth) are protected or dampened from disturbances that affect shallow reefs (<30 m), such as pollution, unregulated tourism,
and overfishing (Bongaerts et al. 2010). The DRRH was firstly related to global warming and its massive, but non-uniform effects on coral bleaching and mortality (Hoegh-Guldberg 1999); some benign habitats, such as deep, sunlit reef substrates, oceanic shoals, and relatively high-latitude locations, might escape from increased sea surface temperature and offer refuge for coral populations (Glynn 1996). As the DRRH gained attention, evidence from mesophotic coral ecosystems suggested that the deep reefs could also act as a viable reproductive source for shallow reef areas following disturbance, expanding the notion of thermal refuge to source of propagules as well (Lesser et al. 2009, Bongaerts et al. 2010, Loya et al. 2016). Yet, this possibility is under intense debate (Prasetia et al. 2017, Shlesinger et al. 2017).

Despite many researchers have discussed their results in light of the DRRH framework (Lesser et al. 2009, Bongaerts et al. 2010, Loya et al. 2016), the number of studies explicitly designed to validate the assumptions or test the predictions of the DRRH is still limited (Smith et al. 2016, Bongaerts et al. 2017, Semmler et al. 2017). For instance, the assumption that cooler environments protect corals from bleaching has been recently challenged, as Caribbean mesophotic corals (30–75 m depth) have lower bleaching threshold temperatures than shallow corals (Smith et al. 2016). Similarly, the prediction of high vertical connectivity between deep and shallow reefs has been genetically supported for the broadcasting species Stephanocoenia intersepta, but not for the brooding species Agaricia fragilis (Bongaerts et al. 2017). Mixing results have been also reported at the community level (Riegler and Piller 2003, Semmler et al. 2017), revealing the need for more explicit evaluations of this important hypothesis.

When genetic flux is detected across populations of shallow and deep areas, the set of subpopulations may comprise a metapopulation in which the deep areas serve as refuges (Bongaerts et al. 2010 and references therein). The same rationale can be scaled up to the community level if depth-generalist species connect shallow and deep reefs. Such connectivity assumes that the shallow-deep continuum encompasses a meta-community, that is, a set of local communities (coral reefs) that are linked by dispersal of multiple interacting species (Leibold et al. 2004). If the DRRH holds, this metacommunity is expected to follow a mass-effect model in which immigration and emigration allow species to be rescued from local competitive exclusion in unsuitable sites (Leibold et al. 2004). Under this scenario, species more adapted to the conditions of shallow reefs could maintain smaller populations in deep reefs and vice versa, making the metacommunity dominated by depth-generalist species.

The reefs of the tropical Southwestern Atlantic province, along with those of the North Brazil shelf, comprise the largest and richest reef formation of the South Atlantic Ocean (Spalding et al. 2007, Leão et al. 2016). The Brazilian coral fauna is low compared to the Caribbean reefs, being currently represented by 23 scleractinian species, five hydrocorals, and 22 species of octocorals (Castro et al. 2010, Leão et al. 2016). In contrast to the shallow reefs, the mesophotic coral ecosystems of the Southern Atlantic are still poorly studied (Oliveira Soares et al. 2016). Even with the recent advances in the deep reefs of oceanic islands (Amado-Filho et al. 2016), submarine mountains (Meirelles et al. 2015), and the mouth of the Amazon river (Cordeiro et al. 2015), the potential role of deep reefs to serve as refuges for coral communities has been not yet assessed.

In this study, we test the DRRH using a community-level approach able to partition the coral gamma diversity into independent alpha and beta components (Jost 2007). We sample coral communities in 19 reefs of the Northeastern Brazil ecoregion (Spalding et al. 2007) to test five predictions supporting the DRRH. The first prediction was that deep reefs should host greater gamma diversity to be able to export species to shallow reefs. Second, depth-generalist species should dominate the shallow reefs; otherwise; local extirpation in shallow areas could not be reverted by the deep reefs. Third, alpha diversity should be greater in deep reefs due to reduced anthropogenic pressure in deeper areas. Fourth, beta diversity should be smaller among shallow than deep reefs due to the human-induced spread of a few disturbance-adapted species near sea surface. Finally, to serve as refuges, deep reefs should encapsulate the functional attributes (e.g., reproduction mode, type of skeleton, sexuality) observed in shallow reefs to ensure functional recovery of shallow reefs. As a preambule,
we describe the substrate cover, the taxonomic composition along the depth gradient, and report new records for the region.

Methods

Study area

We conducted the study in the eastern coast of Northeast Brazil near the metropolitan region of João Pessoa, state of Paraíba (Fig. 1). The continental shelf in this area is relatively short (35-km wide), most of it lies at depths smaller than 40 m and the break occurs at 75 m (O. A. Silva, B. A. Santos, and T. C. M. Araújo unpublished data). Water temperature is relatively constant around 28–29°C up to the 50 m; after this depth, a sharp thermocline of unknown seasonality reduces the temperature to about 23–24°C (Feitoza et al. 2005). The shallow reefs of this and other tracts of the Northeastern Brazil ecoregion are relatively well studied; some reefs are attached to the coast, and others are several kilometers offshore, generally lying parallel to the coast at depths of approximately 5–10 m (Leão et al. 2016). The deep reefs of the region, on the other hand, are virtually unknown. The only study developed so far (Feitoza et al. 2005) describes the fish communities of 14 reefs between 35 and 70 m depth and concludes that the deep reefs may function as a faunal corridor between southeastern Brazil and the Caribbean.

Data survey

To identify the reefs to be surveyed within the limits of our study area, we first consulted fishermen and local dive operators on possible reef locations. Then, we confirmed the locations with exploratory SCUBA dives and bathymetric data from a portable hydrographic echo sounder system (SonarMite), which located potential

Fig. 1. Study region in the coast of Paraíba, Northeast Brazil, showing an example of shallow (<30 m depth, green circles) and deep reefs (>30 m depth, red triangles).
Sample coverage and diversity metrics

To compare the coral diversity across the depth gradient, we first assessed the inventory completeness of each reef using the coverage estimator recommended by Chao and Jost (2012) (Appendix S1). To partition the diversity into independent alpha and beta components, we used multiplicative diversity decompositions of effective numbers of species (so-called Hill numbers, $\hat{D}$) in its unweighted form (Jost 2007). We considered diversity of rare ($\hat{D}$), typical ($\hat{D}$), and dominant ($\hat{D}$) species (Appendix S2).

**RESULTS**

Overall, coral cover was low, 3.4% on average, varying from 0.3% to 20.2%. Reef cover was largely dominated by rock with 38.9% (1.4–79.5%; minimum–maximum), followed by macroalgae (31.4%; 2.3–95.8%), sand (15.2%; 0.3–43.5%), and sponges (1.0%; 0.4–5.4%), plus 10.1% undistinguishable cover. We recorded 861 coral colonies belonging to 17 species and 14 families: 11 scleractinian species, one octocoral, one black coral, one hydrocoral, and three zoanthids (Appendix S3). The scleractinian coral Agaricia fragilis and the black coral Cirripathes sp. represented new records for the state of Paraiba, Brazil. The most abundant species were the reef-building, depth-generalists Siderastrea stellata (74.7% of the colonies) and Montastraea cavernosa (18.5%). Only three species occurred along the entire gradient of depth: S. stellata, M. cavernosa, and Mussismilia hispida. Ten species were observed only in the shallow reefs (>58% of the regional richness), while four occurred exclusively in the deep reefs (Fig. 2).

The three metrics of alpha diversity ($\hat{D}$, $\hat{D}$, $\hat{D}$) varied from one to five species per reef but did not respond to depth (Fig. 3). Compared with deep reefs, shallow reefs showed 50% more beta diversity of rare species ($\hat{D}$; 4.5 vs. 3.0 communities) and 30% more beta diversity of dominant species ($\hat{D}$; 1.6 vs. 1.2 communities; Fig. 4). This greater beta diversity also resulted in greater gamma diversity in shallow reefs, which almost doubled the gamma diversity recorded in the deep areas (13 vs. 7 species).

Because S. stellata and M. cavernosa dominated the depth gradient, the metacommunity was dominated by reef-building, zooxanthellated, gonochoric corals with brooding or broadcast reproductive mode. However, soft corals were observed only in shallow reefs and azooxanthellated corals were recorded only in deep reefs.

**DISCUSSION**

Our community-level approach using southwestern Atlantic coral communities provides...
little support to the DRRH, as four of the five DRRH predictions were not corroborated. Our analyses demonstrate that coral communities of shallow and deep reefs exhibit similar levels of alpha diversity, but species turnover is greater in shallow areas, resulting in twice more gamma diversity at lower depths. This contradicts DRRH expectations for alpha, beta, and gamma diversity. In addition, only three species were depth-generalists and 58% of all species were restricted to the shallow reefs. This means that more than half of the coral diversity in the region may be locally extinct if conditions become unsuitable for shallow-specialists. Nonetheless, with the exception of soft skeleton, all functional attributes of shallow reefs were present in deep reefs due to the dominance of the depth-generalists *Siderastrea stellata* and *Montastraea cavernosa*. It is worthy to mention that our deep reefs were in the upper limit of the mesophotic zone (up to 61 m), where the differences between shallow and deep areas should be minimum according to the DRRH (Loya et al. 2016).

The coral metacommunity comprised by the 17 species do not follow a mass-effect model as expected by the DRRH. Rather, it follows a species-sorting model in which two species...
dominate the local communities anywhere in the region (S. stellata and M. cavernosa), while the other 15 species are separated into spatial (depth) niches (Leibold et al. 2004). Sedimentation and turbidity, common in shallow and deep reefs of our region, are known to negatively affect corals and select a few species more adapted to the stressful conditions (Erftemeijer et al. 2012). Montastraea cavernosa is recognized for its high capacity of sediment removal and is among the most important reef-building corals of the South Atlantic and the Caribbean (Francini-Filho et al. 2013, Leão et al. 2016). Its physiological and morphological adaptations to tolerate greater depths have been documented as well (Esser et al. 2010). Siderastrea stellate, by far the most abundant coral species in our region, seems to be even more tolerant to depth, sedimentation, and turbidity (Souza and Amaral 2002, Leão et al. 2003). These characteristics certainly explain its ecological success throughout the coast of Paraíba and other Brazilian reefs, such as the Vitória-Trindade seamount chain (Meirelles et al. 2015), Abrolhos bank (De Moura et al. 2013), Rocos Atoll (Amado-Filho et al. 2016), and other mesophotic reefs of Northeast Brazil (Oliveira Soares et al. 2016).

Several factors, besides depth, might be involved in coral distribution and explain the deviation from the DRRH predictions. One possibility is that competition for consolidate substrate (Liddell and Avery 2000) and/or level of human disturbance (Appeldoorn et al. 2016) were greater in deep than shallow reefs. However, most reef surface of shallow and deep reefs was uncovered and classified as rock (see smaller rock cover in Bridge et al. 2011, Meirelles et al. 2015, Cordeiro et al. 2015), indicating that there would be enough space for corals to expand their cover by 10 times at any depth. In addition, there is no evidence supporting increased pressures of fishing, pollution, and tourism on the deep reefs (Leão et al. 2003). In fact, these threats are more common in shallow areas due to the proximity from the coast. Thus, the depth—and its intrinsic covariates (i.e., light, pressure, temperature)—is more likely to be the main driver of community organization at our study region.

Besides species sorting into depth niches, the geographic (horizontal) distance between the shallow and deep reefs might be involved in the striking taxonomic differentiation between the shallow and deep reefs. While the shallow reefs were attached to the coast or less than a kilometer offshore, the deep reefs were often more than 20 km offshore. This horizontal gap is likely to favor the depth specialization in the region, as larval dispersion may be as short as 100 m (Underwood et al. 2007), and drastically reduce the supposed reseeding potential of deep reefs (Hinderstein et al. 2010).

The greater beta diversity of shallow reefs was quite surprising, given that the human pressures close to the coast should have homogenized the coral communities at lower depths (Leão et al. 2003). This could be driven by simple distance decay if the deep reefs were less distant and more similar to each other than the shallow reefs. However, our deep reefs were actually 26.7 km apart from each other (on average), while the shallow reefs were closer, 15.5 km apart from each other. Also, there was no significant effect of geographic distance on species composition (Appendix S2). Thus, the geographic distance per se is unlikely to generate the beta diversity patterns within the group of shallow reefs.

Fig. 4. Beta diversity of rare ($q = 0$), typical ($q = 1$) and dominant ($q = 2$) coral species across communities in shallow (<30 m) and deep (>30 m) reefs of Northeast Brazil.
Apparently, the shallow-specialist species are sorted by differences in patch quality from one reef to another (Leibold et al. 2004), such as different pressures from tourism and fishing activities, but this possibility remains to be examined.

Our analyses indicate that the DRRH is likely to hold for the two dominant, depth-generalist S. stellata and M. cavernosa, which requires further population-level analyses. One possibility for measuring the capacity of mesophotic populations to replenish shallow reefs after disturbance is to measure the extent and direction of gene flow between these habitats (Van Oppen et al. 2011). To this end, the characteristics of each species will ultimately determine its success in connecting shallow and deep reefs. For example, the large eggs of M. cavernosa can increase the survival time of the larvae, its dispersal capacity, and survival (Nunes et al. 2009). But studies that tested this ability demonstrate that vertical connectivity can vary greatly between species within the same reef (Bongaerts et al. 2017) and within the same species but at different reefs (Serrano et al. 2014). We encourage further studies to investigate gene flow of M. cavernosa and S. stellata among reefs at the same and different depths in our study region to quantify the level of horizontal and vertical connectivity of shallow and deep reefs.

**Conclusions**

In summary, the deep reefs are unlikely to serve as refuges for Southwestern Atlantic coral communities that face human pressures at lower depths. If any, they have potential to replenish shallow reefs with only two depth-generalist species, Siderastrea stellata and Montastrea cavernosa. Because beta diversity is very high, especially in shallow reefs, and many species are specialized in particular depths, conservation actions in the region should integrate the protection of shallow and deep reefs to maintain the regional coral diversity.

**Acknowledgments**

We thank the Fundação Grupo O Boticário de Proteção à Natureza (Grant number 1044-20152) for funding this study and the Mar Aberto Dive Center for logistical support. The Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) provided research grant to Bráulio Santos (310340/2016-0) and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) provided a graduate scholarship to Juliano Morais. Technical divers Orione Alvares da Silva, Michel Russi, and Ismar Just supported the fieldwork. We also thank three anonymous reviewers for helpful comments on earlier drafts of the manuscript and the team involved in the production of the documentary Unidades de Mar (Marine Protected Areas), freely available at https://youtu.be/72w4b1ZVBDM.

**Literature Cited**


Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2281/full