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Marginal coral reefs show high susceptibility to phase shift

Igor C.S. Cruz[a,b,*], Linda G. Waters[a], Ruy K.P. Kikuchi[b], Zelinda M.A.N. Leão[b], Alexander Turra[a]

[a] *Laboratório de Manejo, Ecologia e Conservação Marinha, Departamento de Oceanografia Biológica, Instituto Oceanográfico, Universidade de São Paulo, Praça do Oceanográfico, Butantã, Instituo Oceanográfico, Sala 112, 055080-120 São Paulo, SP, Brazil*
[b] *Departamento de Oceanografia, Instituto de Geociências, Universidade Federal da Bahia. Rua Barão de Geremoabo, s/n Ondina, 40170-115 Salvador, BA, Brazil*

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ABSTRACT

Phase shift, resulting from coral reef degradation, has been frequently recorded on reefs in optimal conditions, while marginal reefs were considered more resistant due to few records. Noting the lack of marginal reef phase shift studies, we quantitatively assessed their geographic extent in the Southwest Atlantic. Using metadata and a calculated phase shift index, we identified phase shifts from corals to both zoanthid and macroalgal dominance. Positive correlations existed between phase shift and local human impacts for zoanthids: proximity to human populations > 100,000 inhabitants, urbanized surfaces and dredged ports and a negative relationship to the endurance of SST > 1 °C above normal. Macroalgal shifts positively correlated to ports and urbanized surfaces, higher latitudes and shore proximity, indicating a possible link to nutrient runoff. The high frequency of these phase shifts suggests greater degradation than reported for Caribbean reefs, suggesting that marginal reefs do not have higher natural resistance to human impacts.

1. Introduction

Coral reefs provide several substantial ecological services, such as fishing, coastline protection and tourism, have economic value (Costanza et al., 2014) and contain inherent high biodiversity (Connell, 1978) and productivity (Birkeland, 1997). Human activities have damaged coral reefs over the past five decades (Burke et al., 2011; Hughes et al., 2017). This damage reached a level that was described as a "coral reef crisis" (Bellwood et al., 2004; Madin and Madin, 2015), with 20% of reefs degraded globally and an additional 35% threatened as of 2008 (Wilkinson, 2008) and 75% of global coral reefs threatened in some way as of 2010 (Burke et al., 2011; Hughes et al., 2017).

The most drastic consequence of coral reef degradation is the "phase shift" phenomenon (Graham et al., 2014; Hughes et al., 2017). In coral reefs, a phase shift is a change in dominance from reef-building corals to non-reef building groups such as macroalgae or sponges (Done, 1999; Norström et al., 2009). This phenomenon can result from either natural or anthropogenic disturbances (Cruz et al., 2014; Dudgeon et al., 2010). The resulting loss of reef-building capacity could cause the loss of structural complexity (Graham et al., 2014). As a consequence, the reef could lose the capacity to maintain its local diversity (Graham et al., 2015; Harborne et al., 2011; Letourneur et al., 2017) due to loss of habitat heterogeneity and structural complexity, altering trophic structure (Cruz et al., 2015b; Done, 1999; Hempson et al., 2018), harming the structural integrity of the reef over the long-term (Feary et al., 2007) and causing loss of ecosystem services (Bellwood et al., 2004; Graham et al., 2014).

For effective management and mitigation of reef degradation, data that extends geographically across the region of study is necessary to make inferences about regional patterns. The current condition of reefs of interest should be assessed, then cross-referenced with potential local impacts. Faced with a forecast of an increase in phase shift phenomena due to climate change and human activities, a better understanding has become crucial (Hughes et al., 2017; Roff and Mumby, 2012). For macroalgal shifts, a global overview was conducted (excluding the east coast of Africa, Red Sea and Persian Gulf) (Bruno et al., 2009). Such studies on a regional scale, which allow correlation with local impacts, have only been conducted in the Florida Keys, Great Barrier Reef and Hawaiian archipelago (Bruno et al., 2009; Jouffray et al., 2014).

Marginal reefs, those living at the limit of tolerable environmental conditions (e.g. temperature, salinity, light, carbonate saturation state, and/or nutrients) (Perry and Larcombe, 2003), are important because of their potential as an ecological refuge and could be more resistant to effects of climate change than the non-marginal ones due to their more flexible and resistant community of organisms (Couce et al., 2013; Freeman, 2015). By comparing phase shift rates on these reefs to our

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* Corresponding author at: Laboratório de Manejo, Ecologia e Conservação Marinha, Departamento de Oceanografia Biológica, Instituto Oceanográfico, Universidade de São Paulo, Praça do Oceanográfico, Butantã, Instituo Oceanográfico, Sala 112, 055080-120 São Paulo, SP, Brazil.
E-mail address: igorcruz@usp.br (I.C.S. Cruz).

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understanding of those under optimal conditions, we could potentially identify differences in the incidence and severity of phase shifts, along with differences in potential recovery rates for these two types of reef systems. Specific localized incidences of phase shifts have been noted in a few marginal reef systems, such as those in the Keppel Bay, Australia, at the upper limit of light attenuation tolerance for a coral reef (Bennett et al., 2010), Whitsunday Island, Australia, at the upper limit of tolerance to sedimentation and water pollution (DeVantier et al., 1998) and Boca del Toro in Panama, also at the upper limit of tolerance to sedimentation and pollution (Schlöder et al., 2013). Past regional studies of phase shifts, in contrast, have almost exclusively concentrated on reefs under "optimal" conditions, such as in the Florida Keys, Hawaii, and the Great Barrier Reef (Bruno et al., 2009; Jouffray et al., 2014). The lack of regional studies on marginal reefs could have placed a potential bias on the current understanding of how these coral reefs will likely respond to environmental change (Suggett et al., 2012), as conflicting phenomenon have been reported in individually studied locations. While some temperate ecosystems undergo "tropicalization", where areas usually dominated by algae become dominated by hard corals due to a long-term temperature increase (Figueira and Booth, 2010; Tuckett et al., 2017), others that remain outside coral tolerance limits for additional environmental conditions besides temperature could induce a phase not dominated by corals from that same rise in temperature.

To put phase shifts in the context of geographic effects and a wider range of environmental pressures, this work is a comprehensive examination of the large-scale system of reefs under marginal conditions along the Brazilian coast (0°40′S to 19°40′S). These Southwest Atlantic coral reefs are considered a marginal ecosystem, with corals living at the limit of sedimentation tolerance (Suggett et al., 2012). They occupy approximately 2900 km along the tropical coast; the lateral extent of the reefs across the narrow Brazilian tropical continental shelf is uncertain. Reef area estimates vary from 1200 km^2 in total (Spalding et al., 2001) to 8844 km^2 for only the Abrolhos Bank region, which extends along 10% of the coastline (Moura et al., 2013). We note that while Bruno et al. (2009) included some of the older macroalgal shift data from Brazil in a phase shift study, only data from the reef check program was included. Those reefs were examined jointly with reefs in the Caribbean Sea, complicating any region-specific conclusion. Most of the available data for the region was excluded, as it was sampled with other methods, such as AGRRA, video transects and photo-quadrats. A comprehensive examination of this region could be used as an indicator of potential future effects on non-marginal reefs around the world.

We re-examined studies along the coast of Brazil to identify potential phase shift phenomena occurring on Southwest Atlantic marginal reefs, evaluate the extent of phase shifts, understand their potential environmental and anthropogenic drivers, and look for evidence of temporal variation in the reef conditions when possible. A few studies have described phase shifts on Southwest Atlantic coral reefs (Bruce et al., 2012; Cruz et al., 2015a; Feitosa and Ferreira, 2014; Pereira et al., 2014). Other studies in Brazil have included descriptions of reef benthic assemblages that have a pattern compatible with the concept of a phase shift (Costa et al., 2008; Costa et al., 2002; Kikuchi et al., 2010; Loiola et al., 2014; Medeiros et al., 2010), which will be included in our analysis.

2. Methods

In the absence of baseline studies of the historical state of Southwest Atlantic coral reefs, we used two key underlying assumptions to identify phase shifts. First, that historically "normal" or "healthy" coral reefs are dominated by reef-building organisms (≥25% for functional dominance cf. Bruno et al. (2009), noting however that the current highest averages among coral cover estimates in the Southwest Atlantic are 13% in Todos os Santos Bay cf. Cruz et al. (2015a) and 12% for the offshore Abrolhos Bank cf. Leão et al. (2010)). Second, that non-reef-building organisms were relatively scarce (Bruno et al., 2009) on those reefs for them to have been constructed; a shift in reef dominance has been recorded between baseline and subsequent studies at other sites such as in Jamaica (Done, 1992) and Panama (Schlöder et al., 2013). Thus, we assumed that dominance by non-reef-building organisms in this benthic community indicated that a phase shift has occurred. Although it has been suggested that persistence of the phase shift for a minimum of five years is also necessary (Norström et al., 2009), we will not consider it here due the absence of consensus (Dudgeon et al., 2010) and the scarcity of temporal data in this region.

We reviewed all available studies regarding Southwest Atlantic coral reefs containing benthic community data up to April 24th, 2015 using the ISI Web of Science and Scopus databases, searching "coral reef degradation Brazil", "coral reef community Brazil" and "Benthic reef Brazil". We restricted our analysis to the subset of studies that contained coral cover data (including scleractinean and calcareous hydroids) and coverage data for turf algae, macroalgae, zoanthids, or sponges. These studies contained variations in the groups of organisms recorded as they were sampled with one of four different methods: the AGRRA Protocol version 3.0, line point intercept including Reef-Check, quadrats and video-transects. We extracted these data from text, tables, or from the graphs (using a caliper ruler), measuring their values against the scale of their coverage axis. We discarded data from the intertidal zone, wishing to eliminate any confounding of results from tidal effects and air exposure. We also discarded data that was duplicated by another of the selected studies, keeping the more recent of the datasets from any site when sampled with the same sampling method. However, we retained data from the same site if obtained with different methods because inherent biases in each method mean that the organism percentage estimates will not be identical. We also noted if these studies specifically discussed or recorded a phase shift. We found 96 studies (Supplementary material 1) but only 22 fit our restriction, providing a total of 121 sites (Supplementary material 2).

We evaluated the condition of reefs by calculating separate Phase Shift Indices (PSI) (Bruno et al., 2009) for four non-reef-building organisms (turf algae, macroalgae, zoanthid or sponge). As phase shift involves many different rates of coral loss and non-reef-building organism group increases, it can be considered a multivariate phenomenon (Graham et al., 2006). The purpose of the PSI is to facilitate graphical representation and statistical comparison, simplifying contrasts between reefs and between different types of studies. For this, we reduced a matrix with coral cover and coverage of that particular non-reef-building organism to a single value using the first component in a Principal Component Analysis (PCA) (cf. Bruno et al., 2009; Jouffray et al., 2014) to create the Phase Shift Index values. For each PSI, the first variable was assigned to the non-reef-building organism coverage and the second to coral cover to simplify interpretation, so that coral cover decreased with increasing PSI. Because the reviewed studies used distinctly different methods, missing data for one or more variables is both common and differs by study, we thus analyzed these four non-reef-building organisms separately. Each type of organism being compared to coral cover thus uses a slightly different subset of sites for which all data is available. The Principal Component Analyses (PCA) used to calculate PSIs were performed using Stat Soft Statistica version 8.0.

These PSI values represent the current condition of each reef at the time of survey; they can only show a temporal change on a specific reef if a time series is available. All calculated PSIs ranged from −3 to 4. A negative PSI indicates a reef in "pristine" condition, with high coral cover and low non-reef-building organism coverage. A positive value indicates low coral cover and high non-reef-building organism coverage. When coverage for both organisms decreases with increasing PSIs (both negative), this indicates that both organisms are declining in conjunction but not that a third organism or set of organisms are now taking over the occupying of that space. In this situation, because this third organism or set of organisms were unidentified due to lack of comprehensive coverage data, the PSI of the non-reef-building