

Opinion Paper

Marginal reef paradox: A possible refuge from environmental changes?

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ABSTRACT

The occurrence of coral reef communities under extreme and different-from-optimum conditions makes it possible to test hypotheses about resilience in the face of increasing local and global impacts. Recently, coastal marginal reefs have been hypothesized to provide refugia from natural and anthropogenic impacts. Herein, I present empirical evidence contradicting this assumption and explain a new idea, called the “marginal reef paradox”. The marginal reef paradox has two main contradictory concepts. First, the hypothesis that marginal reefs may be more resilient to global changes (such as global warming and heat waves) but less resilient to local ones (such as overfishing, runoff, local pollution, dredging, river discharge, and habitat destruction). Second, that despite the resilience to thermal stress, the marginal reefs are not refugia to other reef ecosystems owing to their vulnerability and because these reefs significantly differ from their tropical counterparts. Thus, marginal reefs such as turbid-zone and high-latitude reefs are ecologically distinct ecosystems and represent limited potential as refugia for other reef ecosystems. I also argue that marginal reefs are under severe anthropogenic pressure and in as much need of conservation actions as “classical” coral reefs. Moreover, their resilience will be lost within the next few decades if proper and urgent conservation actions are not taken.

1. Introduction

The idea that shallow-water coral reefs occur and thrive only in clear and oligotrophic tropical waters with a characteristic temperature range (ca. 20–30 °C) has long been an established paradigm in scientific literature (Hughes et al., 2017). This paradigm arose because most of our knowledge base on the structure and dynamics of reefs was developed from research conducted primarily in the Caribbean Sea and Australia (Mumby, 2009; Hughes et al., 2018). In these regions, “classical” reefs occur like those described in scientific books and outreach materials: ecosystems with a high degree of coral coverage and a significantly high diversity of scleractinian corals. The low nutrient levels, water transparency, and narrow temperature variability in such coastal systems should be optimal for carbonate bioconstruction, as well as for the maintenance of reefs with high productivity, biodiversity (Hughes et al., 2018), and associated ecosystem services (Costanza et al., 2014). However, in the last few decades, increasing information has accumulated in these same regions (Smithers and Larcombe, 2003; Lybolt et al., 2010; Guest et al., 2016; Pizarro et al., 2017) and in other seas (e.g., in the South Atlantic Ocean, Red Sea, NW Pacific, Kuroshio region, Mozambique, and Persian/Arabian Gulf) (Perry, 2003; Nakajima et al.,

2012; Hume et al., 2015; Suzuki et al., 2016; Porter and Schleyer, 2017; Cruz et al., 2018; Kurihara et al., 2019) showing that shallow-water reefs also occur in marginal or sub-optimal conditions (Perry and Larcombe, 2003). These sub-optimal conditions include significant sedimentation rates, turbid waters, high nutrient content (such as phosphorus and nitrogen), high productivity (mesotrophic or eutrophic waters), and/or highly variable temperatures (Kleypas et al., 1999; Perry and Larcombe, 2003; Halfar et al., 2005; Schoepf et al., 2015; Chow et al., 2019).

These coastal marginal reefs have broadened our knowledge of the ecology, distribution, and social and ecological importance of these marine animal forests (*sensu* Rossi et al., 2017). Studying present-day marginal reefs is crucial to further the understanding of marine biodiversity, ecosystem functioning, and carbonate accretion (Hennige et al., 2010). As global environmental change alters seascapes and energy fluxes over seas (Rossi et al., 2019), research into populations surviving within marginal reefs becomes extremely important, as it can provide novel and useful insights into the future scenarios of tropical “classical” coral reefs (Camp et al., 2018).

In addition, the occurrence of reefs under extreme and different-from-optimum conditions makes it possible to test hypotheses about species resilience in the face of increasing local and global

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environmental changes (Woesik et al., 2011; Morgan et al., 2016). Recently, coastal marginal reefs have been hypothesized to provide refugia from natural and anthropogenic impacts (Glynn, 1996; Riegl and Piller, 2003; Cacciapaglia and Woesik, 2015; Guest et al., 2016). Marginal coral communities predisposed to high environmental plasticity have been suggested as potential refuges for their resident populations or immigrant species in a future of warming seas, frequent heatwaves, and ocean acidification (Glynn, 1996; Riegl and Piller, 2003). However, current information on coral refuge environments in marginal environments remains highly debated (Camp et al., 2018).

Herein, I discuss this assumption and explain a new idea, called the “marginal reef paradox.” The marginal reef paradox has two main contradictory concepts. First, the hypothesis that marginal reefs may be more resilient to global changes (such as global warming and heat waves) but less resilient to local ones (such as overfishing, runoff, local pollution, dredging, river discharge, and habitat destruction). Second, that despite the resilience to thermal stress, the marginal reefs are limited refugia to other reef ecosystems owing to their vulnerability and because these reefs significantly differ from their tropical counterparts.

Thus, nearshore marginal reefs (e.g., turbid-zone reefs, high-temperature reefs, and high-latitude reefs) are ecologically distinct ecosystems and represent limited refugia for other reef ecosystems. I argue that marginal reefs are under severe anthropogenic pressure and in as much need of conservation actions as “classical” coral reefs. Moreover, their resilience will be lost within the next few decades if proper and urgent conservation actions are not taken at local and global scales.

2. Summary and evidence as to why marginal reefs were suggested as refuges from ocean warming and heatwaves

Coral reef resilience (or stability) is generally defined as the capacity of a reef to absorb disturbance (i.e., local and/or global impacts such as nutrient pollution or thermal stress) without shifting to an alternative state (phase shift from scleractinian coral to algae, zoanths, sponges, or octocorals) and losing their high-value goods and services (Costanza et al., 2014). This important concept in ecology therefore encompasses two independent processes: resistance—the magnitude of disturbance that causes a change in structure—and recovery—the speed of return to the original structure (Holling, 1996; and reviewed in Côté and Darling, 2010). Thus, resilience has become a core concept in the management of coral reefs worldwide, especially in the face of climate change.

The degradation of “classical” coral reefs overseas (Mumby, 2009; Hughes et al., 2017, 2018) has led to a growing interest in identifying areas that can offer climate-change refugia. Research analyzing resilient or more stable reef populations that already thrive under naturally-occurring marginal physicochemical conditions have therefore become increasingly popular to advance ecosystem scale predictions; however, no single site provides a perfect analog to future coral reefs (Camp et al., 2018).

Coastal marginal reefs have been shown to be more resilient (or more stable) to heat waves and increasing temperatures than reefs that occur under optimum conditions (Leão et al., 2016; Guest et al., 2016; Porter and Schleyer, 2017; Teixeira et al., 2019). Recent evidence suggests that these turbid-zone reefs and the ones at high-latitude have undergone lower rates of bleaching and/or had a higher recovery capacity with lower coral mortality rates after severe thermal stress events (Schleyer et al., 2018; Banha et al., 2019; Teixeira et al., 2019). This resilience based on environmental monitoring or geological studies provides empirical evidence to suggest that marginal reefs could be refuges to warming and heatwaves. For example, Morgan et al. (2017) described higher bleaching tolerance in nearshore turbid-zone corals in Australia following the 2015–2016 warming event, which reinforces their potential to act as a refuge during a prolonged heatwave. Only 1.5% of the studied coral colonies demonstrated partial bleaching, and coral cover after the thermal stress remained unchanged from pre-event measures.

Highlighting this viewpoint, turbidity is one of the factors that can protect corals in turbid-zone reefs (Cacciapaglia and Woesik, 2015) against thermal stress and solar irradiation, and is thus, one of the factors that led to the hypothesis that these marginal reefs represent climate-change refugia. For example, despite the turbid waters they inhabit, some inshore reefs were shown to have higher coral coverage and abundance, larger colonies, and more recruits than those found in more offshore and clearer waters, which was explained by the predominance of sediment-tolerant species in reefs located off the South-western Atlantic coast (Loiola et al., 2019) and Australia (Morgan et al., 2016).

These observations of the greater resilience of nearshore marginal reefs against climate change-related stressors can be explained by a number of adaptations, such as significant heterotrophic rates that compensate for the trophic loss of the coral’s symbionts during bleaching (Mies et al., 2018), protection against light/heat stress by turbidity (Cacciapaglia and Woesik, 2015), and host-symbiont adaptations to variable temperatures (Lien et al., 2007; Hume et al., 2015; Ng and Ang Jr. 2016) (Fig. 1). Common survivorship traits expressed by scleractinian corals within such marginal reefs include phenotypic plasticity, maintenance of energy reserves (e.g., enhanced heterotrophy), and genetic diversity (Camp et al., 2018). The marginal reefs generally comprise and are dominated by disturbance-tolerant massive coral species, algae, and other stress-tolerant benthic suspension feeders (e.g., sponges, octocorals, ascidians, and bryozoans), which increase the ability of an ecosystem to resist the impacts of climate disturbance (Côté and Darling, 2010). Moreover, it is well-known that massive coral species are typically more tolerant to light and heat stress (Camp et al., 2018).

All these ecophysiological characteristics shaped by the host-symbiont association and functional coral traits provide empirical evidence to the hypothesis that marginal coral communities are refuges to thermal stress (Fig. 1). For example, analyzed the response of the coral holobiont to thermal stress in stress-tolerant corals from the northern Red Sea. Their results demonstrated species-specific responses, however, maintenance of energy reserves and heterotrophic feeding appear to be important functional traits to explain thermal tolerance in nearshore marginal reefs. Other evidence was provided from the world’s hottest coral reef (Bento et al., 2016). The Persian Gulf has marginal reefs dominated by massive stress-tolerant corals such as Poritidae and Faviidae. Despite being less diverse and spatially complex, these communities in marginal reefs appear to be resilient to ongoing human impacts (Bento et al., 2016).

3. Evidence and examples where marginal reefs are shown to be vulnerable to anthropogenic impacts

Despite the recognized resistance of marginal reefs to thermal stress which partly supports the “marginal reef paradox,” recent empirical evidence also indicates that the coastal marginal reefs will lose their resistance to light-heat stress owing to the local impacts, increasing warming and more frequent heatwaves predicted in the next years (Fig. 2). For example, bleaching events affected 20 species of scleractinians, hydrocorals, octocorals, and zoanths in SW Atlantic turbid-zone reefs over the last 25 years since 1994 to 2019 (Soares et al., n.d.). Despite the anomalies in sea surface temperatures, higher degree heating weeks, and high rates of coral bleaching (e.g., up to > 60%), these reefs have not exhibited mass mortalities after these events (Leão et al., 2016; Banha et al., 2019; Teixeira et al., 2019). However, in 2019, some reefs in the SW Atlantic (e.g., the Abrolhos bank, Brazil) suffered a severe bleaching event due to an El Niño event with the record of post-bleaching mass mortality in some species (e.g., *Millepora alcicornis*).

Furthermore, considering the projected ocean-climate change in IPCC (Intergovernmental Panel on Climate Change) scenarios, Mazzucco et al. (2019) suggest that recruitment of marine populations in marginal turbid-zone reefs could be highly sensitive to climate change in the

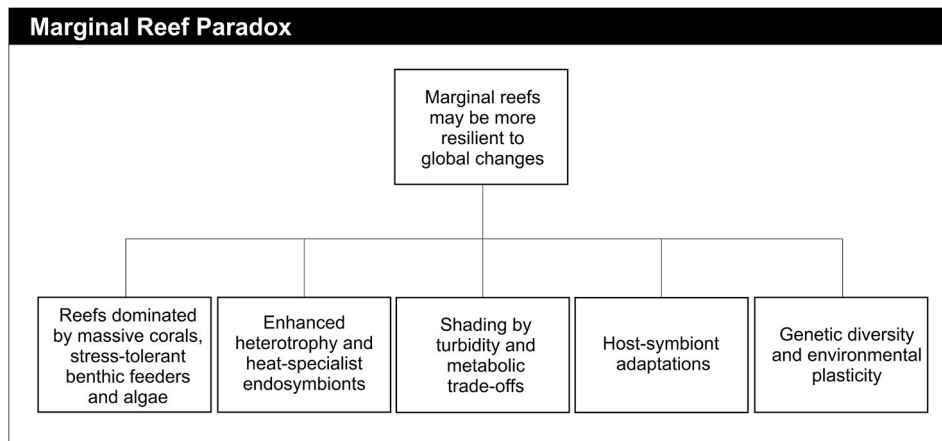


Fig. 1. Resilience of nearshore marginal reefs against climate change-related stressors (e.g., heatwaves and warming).

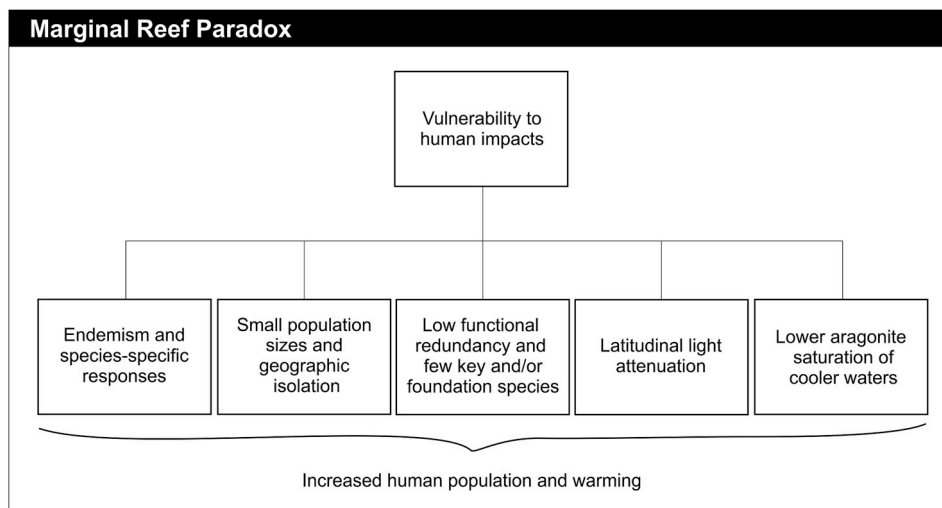


Fig. 2. Marginal reefs: vulnerability to human impacts.

tropical SW Atlantic. In addition, [Fine et al. \(2019\)](#) argued that despite the past bleaching events and higher temperatures, marginal coral reefs in northern sections of the Red Sea are considered reef refugia from global warming and acidification, at least for the coming decades. [Burt et al. \(2019\)](#) also recently found, in the Persian Gulf region, impacts on coral communities (the already rare *Acropora* which were locally extirpated in summer) due to the longest and most severe thermal stress recorded in 2017.

Turbidity is one of the factors that can protect corals by shading against light-heat stress and is thus, one of the factors that led to the hypothesis that these marginal reefs represent climate-change refugia. However, the limit of this resilience against thermal stress is variable but is probably related to the composition of stress-tolerant corals and their functional traits ([Cruz et al., 2018](#)), geographic region ([Burt et al., 2011](#); [Guest et al., 2016](#); [Fine et al., 2019](#)), the magnitude of local anthropogenic impacts ([Cruz et al., 2018](#); [Fisher et al., 2019](#)), and the oceanographic and atmospheric conditions during thermal stress events ([Celliers and Schleyer, 2002](#); [Leão et al., 2016](#)).

Seasonal oceanographic and atmospheric conditions that combine high temperatures during extended periods, low wind speeds, reduced sediment supply to the coast (e.g., during severe droughts or multiple dams on tropical rivers), and reduced water turbulence may decrease the water turbidity during thermal stress events ([Soares et al., 2019a](#)). Although occurring in turbid waters, the occurrence of this combination of conditions over the course of a few months coincident with the

thermal stress may expose corals in marginal reefs to intense mass bleaching events ([Celliers and Schleyer, 2002](#); [Teixeira et al., 2019](#)). For example, [Bahr et al. \(2017\)](#) found that differing local irradiance, precipitation, and turbidity within a bay in a subtropical reef in Hawaii created spatial and temporal variation in bleaching prevalence. Moreover, [Burt et al. \(2019\)](#) showed that 2017 in the Persian/Arabian Gulf reefs was characterized by an extended period of mid-summer calm when winds rarely exceeded breeze conditions, reducing evaporative heat loss, and inducing dramatic warming and mass mortality compared with non-bleaching years (2013–2016). Consequently, these seasonal and spatial variations in oceanographic and atmospheric conditions (combined with heatwaves and warming) indicate that even the refugia against thermal stress provided by turbid-zone or high-temperature marginal reefs are not universal and impervious to impacts, and this can have long-term impacts on the stress-tolerant corals inhabiting them ([Burt et al., 2011](#); [Leão et al., 2016](#)).

Other recent evidence regarding the vulnerability of marginal reefs to anthropogenic impacts is the assumption that there is a limit to the protective function of turbidity against high light ([Fisher et al., 2019](#)) and consequently, to the capacity of turbid-zone marginal reefs to act as refugia. Low-to-moderate decreases in light from suspended sediments can reduce the frequency of coral bleaching, and may reduce mortality, especially for branching corals ([Fisher et al., 2019](#)). However, these authors found that when sediment loads are high, any reductions in bleaching frequency are overwhelmed by increased mortality associated

with severe low light periods and high levels of sediment deposition. The result is that under low sediment inputs the cumulative impact of suspended sediments and thermal stress may be less than expected (antagonistic), whereas at high sediment inputs the aggregate impact is greater than when these stressors occur in isolation (synergistic). Recently, Freitas et al. (2019) also highlighted the deleterious effect of increased turbidity in bioconstruction on marginal reefs. The results of Fisher et al. (2019) and Freitas et al. (2019) emphasize that management of local impacts (e.g., runoff and dredging) may, in some cases, have the capacity to modify their overall impact (including from thermal stress) and undermine the competence of marginal reefs to provide refugia owing to their intrinsic vulnerability.

This clearly suggests that the local anthropogenic impacts that increase sediment runoff and suspended sediments above the limit of marginal reefs is an immediate impact and must be controlled. The increase in suspended sediment concentrations, through urban, agricultural, and industrial runoff; deforestation; resuspension; and dredging activities are an important local source of reef degradation in coastal waters (Fisher et al., 2019; Freitas et al., 2019). These studies provide empirical evidence to the hypothesis of the marginal reef paradox showing the vulnerability of marginal reefs to local impacts, such as elevated suspended sediment concentrations and the synergistic interaction between local and large-scale impacts, which may decrease the overall resilience of marginal reefs.

One of the main empirical evidences in support of the marginal reef paradox is the fact that recent studies suggested that marginal reefs are more highly susceptible to local impacts, such as nutrient runoff, human development, and river discharge (Portugal et al., 2016; Cruz et al., 2018; Freitas et al., 2019), than “classical” reefs like the Caribbean reefs (Fig. 1). Phase shift, resulting from reef degradation, has been frequently recorded in tropical “classical” coral reefs in optimal conditions (Mumby, 2009), while marginal reefs were considered more resistant. However, Cruz et al. (2018) found that 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 (Cruz et al., 2018), suggesting that marginal reefs do not have higher natural resistance, especially to local and regional impacts.

Highlighting this viewpoint, Lybolt et al. (2010) indicated that natural historical instability, coupled with local and regional impacts since European colonization in Australia, severely impacted some marginal reefs, and they thus offer limited potential refuge habitats for reef species. Marginal reefs are not immune to local and regional impacts such as eutrophication-stressed environments. In fact, several recent studies emphasize the need to conserve and protect nearshore marginal reefs from urban and industrial pollution in South China (Chen et al., 2013), contamination in Brazil (Leite et al., 2018), and coastal development and poor water quality in Borneo (Browne et al., 2019) and the Red Sea (Fine et al., 2019). For example, Fine et al. (2019) highlighted the need for immediate action to secure the northern sections of the Red Sea as a coral reef climate change refuge by management and removal of local impacts.

Local impacts, such as urbanization (Schermer et al., 2013; Portugal et al., 2016; Cruz et al., 2018), fisheries (Floros et al., 2013; Giglio et al., 2017), contamination (Cruz et al., 2018; Porter et al., 2018), and dredging (Fisher et al., 2019) degrade coastal turbid-zone and high-latitude marginal reefs. The vulnerability of marginal reefs to local and regional impacts is partly explained by their unique ecological dynamics (Fig. 2). Marginal reefs have lower diversity across seas (Harriott and Banks, 2002; Bennett et al., 2010; Lybolt et al., 2010; Narayan et al., 2015; Bento et al., 2016; Cruz et al., 2018; Browne et al., 2019) than that of “classical” coral reefs, but with significantly high rates of endemism and the presence of species adapted to these harsh conditions (marginal reef specialists). The combination of a few key species, endemism, small population sizes, geographic isolation, and low functional redundancy

in some marginal reefs leads to them having a particular vulnerability (Fig. 2), wherein local and regional impacts that harm these key species (such as fishing, ornamental catches, or pollution) may lead to the instability and degradation of these ecosystems through phase shifts (Cruz et al., 2018), high bioerosion in coral key species (Browne et al., 2019), losses of foundation species (Portugal et al., 2016), and/or the collapse of coastal reef fish biomass (Morais et al., 2017).

The local impacts also interact with the global impacts to undermine the resilience of marginal reefs. For example, strong thermal anomalies, sediment-related stress, and local nutrient pollution (e.g., nitrogen and phosphorus) both interact and act independently to alter coral health in a variety of ways, that finally contributes to disease, bleaching, and mortality of reef-building corals (Wang et al., 2018; Fisher et al., 2019). Camp et al. (2018) suggest that understanding the interaction of multiple stressors, across varying temporal scales, is an important research priority to improve the management and conservation of marginal reefs.

The degradation of coastal marginal reefs because of local and regional impacts and increasing risk associated with thermal stress explained in this section undermines their potential to act as refugia during the Anthropocene. Kavousi and Keppel (2018) proposed criteria to determine the capacity of refugia to facilitate species persistence in reefs, including their long-term buffering capacity, protection from climate change-related stressors, and low exposure to non-climate disturbances such as local and regional impacts. However, marginal reefs do not meet all the above requirements to be refugia owing to the increasing long-term impacts of climate change-related stressors on them, and also the non-climate disturbances that they suffer because of local anthropogenic pressures, such as urbanization, increase in suspended sediments, pollution, and overfishing as reviewed in this section.

4. Limited potential refugia and management options for marginal reefs

Refuge sites are areas that maintain good conditions being lost elsewhere (Kavousi and Keppel, 2018). These could vary across temporal scales, with some environments providing short-term refuge against acute stress (e.g., turbid-zone nearshore reefs reducing irradiance during a bleaching event) vs. long-term chronic changes (e.g., marginal reefs that provide refugia under extreme environmental changes along geological history) (Camp et al., 2018). A marginal reef, to act as a “refuge”, involves patterns and processes that operate at different spatial and temporal scales. Considering an evolutionary time scale (thousands of years), a given marginal reef may have served as refugia for its ecoregion over past environmental conditions (Lybolt et al., 2010). For example, Potts and Jacobs (2000) suggest that turbid-zone coastal areas have provided ecological and evolutionary continuity and refugia for corals during non-reefal periods when physicochemical conditions have been too extreme for coral reef growth.

Nevertheless, considering an ecological time scale (decades), the same marginal reef may be unable to reseed or recover some degraded reefs located in optimal conditions owing to species demographic constraints that reduce recruitment, dispersal, and reproduction. Most research conducted and reviewed with this perspective suggest a short-term (i.e., months or one year) or mid-term (i.e., decades) refuge for its own region/reef during past bleaching events and thermal stress events. However, this does not mean that a marginal reef could act as a long-term refuge for other reef ecosystems in the next years considering increasing warming seas and more frequent heatwaves.

Eakin et al. (2016) suggested that it is currently unclear whether even naturally heat tolerant corals can continue to improve their heat tolerance fast enough to keep pace with global warming, with locations across seas recently suffering intense bleaching. For example, high-latitude marginal reefs and their coral communities are particularly susceptible to climate change. This occurs mainly because of the latitudinal light attenuation, geographic isolation, small population sizes, greater predicted ocean warming, and lower Ω_{arag} of cooler waters

(Beger et al., 2014) (Fig. 2). Furthermore, Camp et al. (2018) also suggested that, to date, it is unclear whether and to what extent high-latitude corals can in fact serve as refugia from continued climate change, despite evidence for some adaptations to their marginal conditions. Although past examples have confirmed the role of marginal reef ecosystems as short-term ecological “refuges”, there is thus far little support that they comprise long-term refugia and/or could be refugia during the ongoing Anthropocene.

Finally, a “refuge” also involves different levels of biological organization, from genes to ecosystems. Even if one species occurs in reefs in optimal and marginal conditions, it does not support the hypothesis that the marginal reef is acting as a refuge for the entire reef including sectors located in optimal conditions. Highlighting this viewpoint, marginal reefs may be ecologically distinct ecosystems and represent limited potential refugia for other reef ecosystems such as “classical” non-marginal coral reefs. Marginal reef species present in such ecosystems (e.g., high-latitude reefs, high-temperature reefs, and turbid-zone reefs) are actually marginal reef specialists, and the diversity of such reefs may be different from that of other coral reefs owing to the high dissimilarity.

Hennige et al. (2010) provided an evidence of this viewpoint within an Indonesian reef system. These authors evaluated coral assemblages along an environmental gradient (e.g., light quality, temperature, and turbidity) that included “optimal”, intermediate, and marginal sites. Coral communities changed across this gradient from diverse, mixed growth form assemblages to specialized, massive growth form dominated assemblages. Branching species *Acropora formosa* and *Porites cylindrica* were only identified at optimal sites. Only one species (the massive coral *Goniastrea aspera*) was identified at the most marginal and optimal sites. Consequently, it suggests refuge only for this particular species and not at the community level owing to the low overlap in species composition. Moreover, even for this species, further analyses need to be conducted such as validation of genetic connectivity and evaluation of reproductive strategies (e.g., fecundity).

Highlighting this opinion, Camp et al. (2018) suggested that knowledge of the connectivity of marginal coral populations relative to adjacent, optimal reefs is a research priority. The capacity to act as refugia will also depend partly on the dispersal of adults and juveniles, with sessile brooding species more likely to exhibit survival and persistence to suboptimal environments over multiple generations compared to broadcast spawning species that may recruit into the suboptimal environment as progeny from “parents” in less stressful reefs (Camp et al., 2018).

Other empirical evidence about the differences in marginal reefs and “classical” reefs and the limitation to act as refugia are supported by empirical evidence provided by research conducted on the marginal high-latitude reefs. These marginal reefs can be considered extreme coral reefs which differ considerably from their tropical counterparts in many ecological aspects (Beger et al., 2014; Camp et al., 2018). The unique diversity of high-latitude marginal reefs is because of the overlap of tropical and temperate species ranges, species that are rare or absent at lower latitudes (where “classical” tropical coral reefs are), strong seasonality in species composition, and a significant number of endemic species (e.g., nestedness) (Beger et al., 2014). Species temporal turnover can be high depending on larval supply and recruitment from lower latitudes and fluctuations in environmental conditions (Beger et al., 2014), and consequently, high-latitude marginal ecosystems are home to an ecologically and functionally distinct reef community.

These patterns of unique diversity and high turnover of species provide evidence that “classical” reefs in optimal sites are ecologically distinct from the marginal reefs, such as turbid-zone and high-latitude reefs. Camp et al. (2018) argued that the heterogeneous nature of reef systems (including marginal and optimal sites) challenges the ability of environments to act as a refuge against multiple abiotic parameters. The same pattern of distinct and heterogeneous ecosystems was recently found between the shallow water and mesophotic reefs in the South Atlantic (Morais and Santos, 2018; Soares et al., 2019b) and

Caribbean/Indo-Pacific reefs (Rocha et al., 2018). Concerning the capacity to act as refugia, this has been shown to be often true for mesophotic reefs, which were initially proposed to be potential refugia for shallow reef species (Morais and Santos, 2018; Rocha et al., 2018).

One of the assumptions of the marginal reef paradox is the vulnerability of coastal marginal ecosystems to local and regional impacts compared to that of “classical” coral reefs indicated by the empirical evidence discussed in this perspective paper (e.g., Portugal et al., 2016; Cruz et al., 2018). Côte and Darling (2010) indicated that management that controls local stressors to reverse degradation and recover original reef species assemblages will actually increase the proportion of sensitive taxa within the community and may decrease ecosystem resilience to climate change. This may be true of “classical” coral reefs that comprise stress-sensitive species across seas (e.g., Caribbean Sea and Indo-Pacific). In contrast, one of the concepts of the marginal reef paradox suggests that coastal marginal reefs are a distinct ecological ecosystem and respond differently than the “classical” coral reefs. The coral communities evolved and naturally comprise stress-tolerant taxa that dominate the community and provide important ecosystem functions, such as the nursery effect and habitat complexity.

Coastal marginal reefs have a higher vulnerability especially if local and regional impacts remove these foundation species. Human pressures that impact vulnerable life history stages, decreasing reproductive output and the supply of recruits essential for coral reef recovery need to be controlled using the best management strategies. Moreover, marginal reefs can be highly vulnerable to the loss of their few foundation or ecoengineering species, as niche specialization or temporal and spatial segregation makes each species unique (i.e., narrow ecological redundancy) (Fig. 2). This pattern was suggested by Mora et al. (2016) and is even more important in the coastal marginal reefs considering the lower diversity of reef-building species than in “classical” coral reefs.

Long-disturbed marginal reefs may evolve by historical processes such as environmental filtering. The environmental filtering theory (Pavoine et al., 2011) assumes that abiotic factors (e.g., higher temperatures, sedimentation, and turbidity) constrain certain traits within limits, resulting in coral species possessing similar traits (Wong et al., 2018) which allow them to survive these suboptimal environmental conditions and shaped marginal reef communities with a higher resilience to climate disturbances such as thermal stresses. However, this process also generates the pattern observed in the marginal reef paradox that the few key foundation species have similar sensitivity to disturbances which increases their risk to local and regional impacts. This pattern also suggests that entire reef functions can be lost because of single disturbances, such as overfishing, habitat destruction, and/or pollution.

Management options include passive conservation strategies, such as the sewage systems in coastal areas, immediate control of runoff, and no-take reserves (marine protected areas) that aim to minimize local and regional impacts. Establishing effective no-take marine protected areas in suitable high-latitude marginal reefs to enhance connectivity along dispersal routes and maintain ecosystem resilience through reduced anthropogenic impacts may be an important strategy (Beger et al., 2014). Moreover, it is very important to avoid the worst management options, such as flawed control of diffuse impacts as fishing, oil spills and impacts from the urban, agricultural, and industrial coastal zones.

5. Is there sufficient evidence to support the claim of a “marginal reef paradox”?

A paradox is a statement or concept that contains conflicting ideas. The marginal reef paradox suggested in this perspective paper has two main concepts as described in the introduction. The marginal reef paradox is supported by empirical evidence discussed in this perspective paper. This evidence comes mainly from research conducted in marginal turbid-zone reefs, high-temperature reefs, and high-latitude reefs distributed around the world. However, more studies are necessary to

verify if some concepts are applied (or not) to other kinds of marginal ecosystems (Camp et al., 2018), where communities survive and flourish, such as macro-tidal reefs, tide-pools, CO₂ vents, *ojos* (low pH springs), mangrove systems, upwelling areas, and mesophotic and deep reefs. Moreover, considering the limited studies on multiple human impacts in distinct marginal reef ecosystems across seas, future research should be conducted to analyze the adherence (or not) to the two core concepts of the marginal reef paradox.

Moreover, the marginal reefs are distinct ecosystems and may only have resilience up to a point, as even thermal- and turbid-tolerant species will have stress limits that may be exceeded by ongoing ocean warming, acidification, and other local and regional impacts such as continental runoff. Their resilience will be lost within the next few decades if proper and urgent conservation actions are not taken. The increased frequency, intensity, and duration of heatwaves and prolonged and continuous global warming (Guinotte et al., 2003; Skirving et al., 2019), ocean acidification (Kurihara et al., 2019), and increased local and regional impacts because of the human population in coastal zones will lead to reductions in the resilience of coastal marginal reefs in the ongoing Anthropocene. Despite the natural resilience of these coastal systems to turbidity, sedimentation, temperature variability, and high nutrient levels, the marginal reef paradox indicates that it is still very important to protect these reefs when their unique characteristics are considered.

Despite current knowledge gaps, marginal coral reefs may have an unrecognized (and disproportionately) high conservation value, owing to the trait selection of resident coral populations adapted to suboptimal conditions. Moreover, marginal environments may offer genetic rescue (e.g., heat-tolerant genotypes across latitudes), which again gives them a high research and conservation value (Camp et al., 2018). How the future seascape of marginal reefs will be shaped by the multiple (local and global) stressors is an important question that must be addressed to reduce and adapt to the diverse impacts on these unique and ecologically distinct reef ecosystems.

The “marginal reef refugia hypothesis” at the community (assemblage) level needs to be tested further using ecological (alfa, beta, and gamma diversity) and genetic connectivity approaches, but the evidence discussed in this perspective paper indicates a limited potential to act as refugia in the Anthropocene. The marginal reef paradox also indicates that if these shallow water reefs are to act as limited refugia in the context of ongoing environmental changes, it is necessary to ensure local and regional conservation actions (i.e. fisheries management and urban development and pollution control) around nearshore marginal reefs, as well as to reduce carbon emissions.

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References

Potts, D.C., Jacobs, J.R., 2000. Evolution of reef-building scleractinian corals in turbid environments: a paleo-ecological hypothesis. In: Proceedings 9th International Coral Reef Symposium (Bali), pp. 249–254.

Bahr, K.D., Rodgers, K.S., Jokiel, P.L., 2017. Impact of three bleaching events on the reef resilience of Kane’one Bay, Hawaii. *Front. Mar. Sci.* 4, 398. <https://www.frontiersin.org/articles/10.3389/fmars.2017.00398/full>.

Banha, T.N.S., Capel, K.C.C., Kitahara, M.V., Francini-Filho, R.B., Francini, C.L.B., Sumida, P.Y.G., Mies, M., 2019. Low coral mortality during the most intense bleaching event ever recorded in subtropical Southwestern Atlantic reefs. *Coral Reefs* 1–17. <https://link.springer.com/article/10.1007/s00338-019-01856-y>.

Beger, M., Sommer, B., Harrison, P.L., Smith, S.D., Pandolfi, J.M., 2014. Conserving potential coral reef refuges at high latitudes. *Divers. Distrib.* 20, 245–257. <https://onlinelibrary.wiley.com/doi/full/10.1111/ddi.12140>.

Bennett, S., Vergés, A., Bellwood, D.R., 2010. Branching coral as a macroalgal refuge in a marginal coral reef system. *Coral Reefs* 29 (2), 471–480. <https://link.springer.com/article/10.1007/s00338-010-0594-5>.

Bento, R., Hoey, A.S., Bauman, A.G., Feary, D.A., Burt, J.A., 2016. The implications of recurrent disturbances within the world’s hottest coral reef. *Mar. Pollut. Bull.* 105 (2), 466–472. <https://doi.org/10.1016/j.marpolbul.2015.10.006>.

Browne, N., Braoun, C., Mcllwain, J., Nagarajan, R., Zinke, J., 2019. Borneo coral reefs subject to high sediment loads show evidence of resilience to various environmental stressors. *Peer J.* 7, e7382 <https://doi.org/10.7717/peerj.7382>.

Burt, J., Al-Harthi, S., Al-Cibahy, A., 2011. Long-term impacts of coral bleaching events on the world’s warmest reefs. *Mar. Environ. Res.* 72 (4), 225–229. <https://doi.org/10.1016/j.marenvres.2011.08.005>.

Burt, J., Paparella, F., Al-Mansoori, N., Al-Mansoori, A., Al-Jailani, H., 2019. Causes and consequences of the 2017 coral bleaching event in the southern Persian/Arabian Gulf. *Coral Reefs* 38 (4), 567–589. <https://link.springer.com/article/10.1007/s00338-019-01767-y>.

Cacciapaglia, C., Woessik, R., 2015. Climate-change refugia: shading reef corals by turbidity. *Glob. Chang. Biol.* 22, 1145–1154. <https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.13166>.

Camp, E.F., Schoepf, V., Mumby, P.J., Hardtke, L.A., Rodolfo-Metalpa, R., Smith, D.J., Suggett, D.J., 2018. The future of coral reefs subject to rapid climate change: lessons from Natural Extreme Environments. *Front. Mar. Sci.* 5, 4. <https://www.frontiersin.org/articles/10.3389/fmars.2018.00004/full>.

Celliers, L., Schleyer, M.H., 2002. Coral bleaching on high-latitude marginal reefs at Sodwana Bay, South Africa. *Mar. Pollut. Bull.* 44 (12), 1380–1387. [https://doi.org/10.1016/S0025-326X\(02\)00302-8](https://doi.org/10.1016/S0025-326X(02)00302-8).

Chen, T., Li, S., Yu, K., 2013. Macrobioerosion in *Porites* corals in subtropical northern South China Sea: a limiting factor for high-latitude reef framework development. *Coral Reefs* 32 (1), 101–108. <https://link.springer.com/article/10.1007/s00338-012-0946-4>.

Chow, G.S.E., Chan, Y.K.S., Jain, S.S., Huang, D., 2019. Light limitation selects for depth generalists in urbanized reef coral communities. *Mar. Environ. Res.* 147, 101–112. <https://doi.org/10.1016/j.marenvres.2019.04.010>.

Costanza, R., de Groot, R., Sutton, P., der Ploeg, S.V., Anderson, S.J., Kubiszewski, I., Farber, S., Turner, R.K., 2014. Changes in the global value of ecosystem services. *Glob. Environ. Chang.* 26, 152–158. <https://doi.org/10.1016/j.gloenvcha.2014.04.002>.

Côté, I.M., Darling, E.S., 2010. Rethinking ecosystem resilience in the face of climate change. *PLoS Biol.* 8 (7), e1000438 <https://doi.org/10.1371/journal.pbio.1000438>.

Cruz, I.C.S., Waters, L.G., Kikuchi, R.K.P., Leão, Z.M.A.N., Turra, A., 2018. Marginal coral reefs show high susceptibility to phase shift. *Mar. Pollut. Bull.* 135, 551–561. <https://doi.org/10.1016/j.marpolbul.2018.07.043>.

Eakin, C.M., Liu, G., Gomez, A.M., De La Cour, J.L., Heron, S.F., Skirving, W.J., 2016. Global coral bleaching 2014–2017: status and an appeal for observations. *Reef Ecol. Count.* 31, 20–26. https://coralreefwatch.noaa.gov/satellite/analyses_guidance/global_coral_bleaching_2014-17_status.php.

Fine, M., Cinar, M., Voolstra, C.R., Safa, A., Rinkevich, B., Laffoley, D., Hilmi, N., Allemand, D., 2019. Coral reefs of the Red Sea – challenges and potential solutions. *Reg. Stud. Mar. Sci.* 25, 100498. <https://doi.org/10.1016/j.rmsa.2018.100498>.

Fisher, R., Bessell-Browne, P., Jones, R., 2019. Synergistic and antagonistic impacts of suspended sediments and thermal stress on corals. *Nat. Commun.* 10, 2346. <https://doi.org/10.1038/s41467-019-10288-9>.

Floros, C., Schleyer, M.H., Maggs, J.Q., 2013. Fish as indicators of diving and fishing pressure on high-latitude coral reefs. *Ocean Coast Manag.* 84, 130–139. <https://doi.org/10.1016/j.ocecoaman.2013.08.005>.

Freitas, L.M., Oliveira, M.D.M., Leão, Z.M.A.N., Kikuchi, R.K.P., 2019. Effects of turbidity and depth on the bioconstruction of the Abrolhos reefs. *Coral Reefs* 38 (2), 241–253. <https://link.springer.com/article/10.1007/s00338-019-01770-3>.

Giglio, V.J., Bender, M.G., Zapelini, C., Ferreira, C.E.L., 2017. The end of the line? Rapid depletion of a large-sized grouper through spearfishing in a subtropical marginal reef. *Perspect. Ecol. Conserv.* 15 (2), 115–118. <https://doi.org/10.1016/j.pecon.2017.03.006>.

Glynn, P.W., 1996. Coral reef bleaching: facts, hypotheses and implications. *Glob. Chang. Biol.* 2, 495–509. <https://doi.org/10.1111/j.1365-2486.1996.tb00063.x>.

Guest, J.R., Tun, K. L.J., Vergés, A., Marzinelli, E.M., Campbell, A.H., Bauman, A.G., Feary, D.A., Chou, L.M., Steinberg, P.D., 2016. 27 years of benthic and coral community dynamics on turbid, highly urbanized reefs off Singapore. *Sci. Rep.* 6, 36260. <https://doi.org/10.1038/srep36260>.

Guinotte, J.M., Buddemeier, R.W., Kleypas, J.A., 2003. Future coral reef habitat marginality: temporal and spatial effects of climate change in the Pacific basin. *Coral Reefs* 22 (4), 551–558. <https://link.springer.com/article/10.1007/s00338-003-0331-4>.

Halfar, J., Godinez-Orta, L., Riegl, B., Valdez-Holguin, J.E., Borges, J.M., 2005. Living on the edge: high-latitude *Porites* carbonate production under temperate eutrophic conditions. *Coral Reefs* 24 (4), 582–592. <https://link.springer.com/article/10.1007/s00338-005-0029-x>.

Harriott, V.J., Banks, S.A., 2002. Latitudinal variation in coral communities in eastern Australia: a qualitative biophysical model of factors regulating coral reefs. *Coral Reefs* 21, 83–94. <https://link.springer.com/article/10.1007/s00338-001-0201-x>.

Hennige, S.J., Smith, D.J., Walsh, S.J., McGinley, M.P., Warner, M.E., Suggett, D.J., 2010. Acclimation and adaptation of scleractinian coral communities along environmental gradients within an Indonesian reef system. *J. Exp. Mar. Biol. Ecol.* 39 (1–2), 143–152. <https://doi.org/10.1016/j.jembe.2010.06.019>.

- Holling, C.S., 1996. Engineering resilience versus ecological resilience. In: Schulze, P.C. (Ed.), *Engineering within Ecological Constraints*. National Academy Press, Washington, pp. 31–44. <https://www.nap.edu/read/4919/chapter/4>.
- Hughes, T.P., Barnes, M.L., Bellwood, D.R., Cinner, J.E., Cumming, G.S., Jackson, J.B.C., Kleypas, J., de Leemput, I.A., Lough, J.M., Morrison, T.H., Palumbi, S.R., van Nes, E. H., Scheffer, M., 2017. Coral reefs in the Anthropocene. *Nature* 546, 82–90. <https://doi.org/10.1038/nature22901>.
- Hughes, T.P., Anderson, K.D., Connolly, S.R., Heron, S.F., Kerry, J.T., Lough, J.M., Baird, A.H., Baum, J.K., Berumen, M.L., Bridge, T.C., Claar, D.C., Eakin, C.M., Gilmour, J.P., Graham, N.A.J., Harrison, H., Hobbs, J.P.A., Hoey, A.S., Hoogenboom, M., Lowe, R.J., McCulloch, M.T., Pandolfi, J.M., Pratchett, M., Schoepf, V., Torda, G., Wilson, S.K., 2018. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* 359 (6371), 80–83. <https://doi.org/10.1126/science.aan8048>.
- Hume, B.C.C., D'Angelo, C., Smith, E.G., Stevens, S.R., Burt, J., Wiedenmann, J., 2015. *Symbiodinium thermophilum* sp. nov., a thermotolerant symbiotic alga prevalent in corals of the world's hottest sea, the Persian/Arabian Gulf. *Sci. Rep.* 5, 8562. <https://doi.org/10.1038/srep08562>.
- Kavousi, J., Keppel, G., 2018. Clarifying the concept of climate change refugia for coral reefs. *ICES (Int. Coun. Explor. Sea) J. Mar. Sci.* 75 (1), 43–49. <https://doi.org/10.1093/icesjms/fsx124>.
- Kleypas, J.A., McManus, J.W., Menez, L.A.B., 1999. Environmental limits to coral reef development: where do we draw the line? *Am. Zool.* 39, 146–159. <https://doi.org/10.1093/icb/39.1.146>.
- Kurihara, H., Wouters, J., Yasuda, N., 2019. Seasonal calcification of the coral *Acropora digitifera* from a subtropical marginal Okinawa reef under ocean acidification. *Coral Reefs* 38 (3), 443–454. <https://link.springer.com/article/10.1007/s00338-019-01794-9>.
- Leão, Z.M.A.N., Kikuchi, R.K.P., Ferreira, B.P., Neves, E.G., Sovieroski, H.H., Oliveira, M. D., Maida, M., Correia, M.D., Johnson, R., 2016. Brazilian coral reefs in a period of global change: a synthesis. *Braz. J. Oceanogr.* 64 (2), 97–116. <https://doi.org/10.1590/S1679-8759201609160645p2>.
- Leite, D.A.C., Salles, J.F., Calderon, E.N., Castro, C.B., Bianchini, A., Marques, J.A., Elsas, J.D.V., Peixoto, R.S., 2018. Coral bacteria-core abundance and network complexity as proxies for anthropogenic pollution. *Front. Microbiol.* 9, 833. <https://doi.org/10.3389/fmicb.2018.00833>.
- Lien, Y.T., Nakano, Y., Plathong, S., Fukami, H., Wang, J.T., Chen, C.A., 2007. Occurrence of the putatively heat-tolerant *Symbiodinium* phylotype D in high-latitude outlying coral communities. *Coral Reefs* 26 (1), 35–44. <https://link.springer.com/article/10.1007/s00338-006-0185-7>.
- Loiola, M., Cruz, I.C.S., Lisboa, D.S., Mariano-Neto, E., Leão, Z.M.A.N., Oliveira, M.D.M., Kikuchi, R.K.P., 2019. Structure of marginal coral reef assemblages under different turbidity regime. *Mar. Environ. Res.* 147, 138–148. <https://doi.org/10.1016/j.marenvres.2019.03.013>.
- Lybolt, M., Neil, D., Zhao, J., Feng, Y., Yu, K.F., Pandolfi, J., 2010. Instability in a marginal coral reef: the shift from natural variability to a human-dominated seascape. *Front. Ecol. Environ.* 9 (3), 154–160. <https://doi.org/10.1890/090176>.
- Mazzucco, A.C., Stelzer, P.S., Donada, G., Bernardino, J.V., Joyeux, J.C., Bernardino, A. F., 2019. Lower diversity of recruits in coastal reef assemblages are associated with higher sea temperatures in the tropical South Atlantic. *Mar. Environ. Res.* 148, 87–98. <https://doi.org/10.1016/j.marenvres.2019.05.008>.
- Mies, M., Güth, A.Z., Tenório, A.A., Banha, T.N.S., Waters, L.G., Polito, P.S., Taniguchi, S., Bicego, M.C., Sumida, P.Y.G., 2018. In situ shifts of predominance between autotrophic and heterotrophic feeding in the reef-building coral *Mussismilia hispida*: an approach using fatty acid trophic markers. *Coral Reefs* 37, 677. <https://doi.org/10.1007/s00338-018-1692-z>.
- Mora, C., Graham, N.A.J., Nystrom, M., 2016. Ecological limitations to the resilience of coral reefs. *Coral Reefs* 35 (4), 1271–1280. <https://link.springer.com/article/10.1007/s00338-016-1479-z>.
- Morais, J., Santos, B.A., 2018. Limited potential of deep reefs to serve as refuges for tropical Southwestern Atlantic corals. *Ecosphere* 9 (7), e02281. <https://doi.org/10.1002/ecs2.2281>.
- Morais, R.A., Ferreira, C.E.L., Floeter, S.R., 2017. Spatial patterns of fish standing biomass across Brazilian reefs. *J. Fish Biol.* 91 (6), 1642–1667. <https://doi.org/10.1111/jfb.13482>.
- Morgan, K.M., Perry, C.T., Smithers, S.G., Johnson, J.A., Daniell, J.J., 2016. Evidence of extensive reef development and high coral cover in nearshore environments: implications for understanding coral adaptation in turbid settings. *Sci. Rep.* 6, 29616. <https://doi.org/10.1038/srep29616>.
- Morgan, K.M., Perry, C.T., Johnson, J.A., Smithers, S.G., 2017. Nearshore turbid-zone corals exhibit high bleaching tolerance on the Great Barrier Reef following the 2016 ocean warming event. *Front. Mar. Sci.* 4, 224. <https://doi.org/10.3389/fmars.2017.00224>.
- Mummy, P.J., 2009. Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. *Coral Reefs* 28 (3), 761–773. <https://link.springer.com/article/10.1007/s00338-009-0506-8>.
- Nakajima, Y., Nishikawa, A., Iguchi, A., Sakai, K., 2012. Regional genetic differentiation among northern high-latitude island populations of a broadcast-spawning coral. *Coral Reefs* 31 (4), 1125–1133. <https://link.springer.com/article/10.1007/s00338-012-0932-x>.
- Narayan, Y.R., Lybolt, M., Zhao, J.X., Feng, Y., Pandolfi, J.M., 2015. Holocene benthic foraminiferal assemblages indicate long-term marginality of reef habitats from Moreton Bay, Australia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 420, 49–64. <https://doi.org/10.1016/j.palaeo.2014.12.010>.
- Ng, T.Y., Ang Jr., P., 2016. Low symbiont diversity as a potential adaptive strategy in a marginal non-reefal environment: a case study of corals in Hong Kong. *Coral Reefs* 35 (3), 941–957. <https://link.springer.com/article/10.1007/s00338-016-1458-4>.
- Pavoine, S., Vela, E., Gachet, S., de Béclair, G., Bonsall, M.B., 2011. Linking patterns in phylogeny, traits, abiotic variables and space: a novel approach to linking environmental filtering and plant community assembly. *J. Ecol.* 99, 165–175. <https://doi.org/10.1111/j.1365-2745.2010.01743.x>.
- Perry, C.T., 2003. Reef development at Inhaca Island, Mozambique: coral communities and impacts of the 1999/2000 southern Africa floods. *Ambio* 32, 133–139. <https://doi.org/10.1579/0044-7447-32.2.134>.
- Perry, C.T., Larcombe, P., 2003. Marginal and non-reef-building coral environments. *Coral Reefs* 22 (4), 427–432. <https://link.springer.com/article/10.1007/s00338-003-0330-5>.
- Pizarro, V., Rodríguez, S.C., López-Victoria, M., Zapata, F.A., Zea, S., Galindo-Martínez, C.T., Iglesias-Prieto, R., Pollock, J., Medina, M., 2017. Unraveling the structure and composition of Varadero reef, an improbable and imperiled coral reef in the Colombian Caribbean. *Peer J* 5, e4119. <https://doi.org/10.7717/peerj.4119>.
- Porter, S.N., Schleyer, M.H., 2017. Long-term dynamics of a high-latitude coral reef community at Sodwana Bay. *Coral Reefs* 36 (2), 369–382. <https://link.springer.com/article/10.1007/s00338-016-1531-z>.
- Porter, S.N., Humphries, M.S., Buah-Kwofie, A., Schleyer, M.H., 2018. Accumulation of organochlorine pesticides in reef organisms from marginal coral reefs in South Africa and links with coastal groundwater. *Mar. Pollut. Bull.* 137, 295–305. <https://doi.org/10.1016/j.marpolbul.2018.10.028>.
- Portugal, A.B., Carvalho, F.L., Carneiro, P.B.M., Rossi, S., Soares, M.O., 2016. Increased anthropogenic pressure decreases species richness in tropical intertidal reefs. *Mar. Environ. Res.* 120, 44–54. <https://doi.org/10.1016/j.marenvres.2016.07.005>.
- Riegl, B., Piller, W.E., 2003. Possible refugia for reefs in times of environmental stress. *Int. J. Earth Sci.* 92, 520–531. <https://link.springer.com/article/10.1007/s00531-003-0328-9>.
- Rocha, L.A., Pinheiro, H.T., Sheperd, B., Papastamatiou, Y.P., Luiz, O.J., Pyle, R.L., Bongaerts, P., 2018. Mesophotic coral ecosystems are threatened and ecological distinct from shallow water reefs. *Science* 361 (6399), 281–284. <https://science.sciencemag.org/content/361/6399/281>.
- Rossi, S., Bramanti, L., Gori, A., Orejas, C., 2017. Animal forests of the world: an overview. In: Rossi, S., Bramanti, L., Gori, A., Orejas, C. (Eds.), *Marine Animal Forests*. Springer, Cham. https://doi.org/10.1007/978-3-319-21012-4_1.
- Rossi, S., Isla, E., Bosch-Belmar, M., Galli, G., Gori, A., Gristina, M., Ingrassio, G., Milisenda, G., Piraino, S., Rizzo, L., Schubert, N., Soares, M., Solidoro, C., Thurstan, R.H., Viladrich, N., Willis, T.J., Ziveri, P., 2019. Changes of energy fluxes in marine animal forests of the Anthropocene: factors shaping the future seascape. *ICES (Int. Coun. Explor. Sea) J. Mar. Sci.* 1, 1–12. <https://doi.org/10.1093/icesjms/fsz147>.
- Scherner, F., Horta, P.A., de Oliveira, E.C., Simonassi, J.C., Hall-Spencer, J.M., Chow, F., Nunes, J.M.C., Pereira, S.M.B., 2013. Coastal urbanization leads to remarkable seaweed species loss and community shifts along the SW Atlantic. *Mar. Pollut. Bull.* 76, 106–115. <https://doi.org/10.1016/j.marpolbul.2013.09.019>.
- Schleyer, M.H., Floros, C., Laing, S.C.S., MacDonald, A.H.H., Montoya-Maya, P.H., Morris, T., Porter, S.N., Seré, M.G., 2018. What can South African reefs tell us about the future of high-latitude coral systems? *Mar. Pollut. Bull.* 136, 491–507. <https://doi.org/10.1016/j.marpolbul.2018.09.014>.
- Schoepf, V., Stat, M., Falter, J.L., McCulloch, M.T., 2015. Limits to the thermal tolerance of corals adapted to a highly fluctuating, naturally extreme temperature environment. *Sci. Rep.* 5, 17639. <https://doi.org/10.1038/srep17639>.
- Skirving, W.J., Heron, S.F., Marsh, B.L., Liu, G., De La Cour, J.L., Geiger, E.F., Eakin, C. M., 2019. The relentless march of mass coral bleaching: a global perspective of changing heat stress. *Coral Reefs* 38 (4), 547–557. <https://link.springer.com/article/10.1007/s00338-019-01799-4>.
- Smithers, S., Larcombe, P., 2003. Late Holocene initiation and growth of a nearshore turbid-zone coral reef: paluma Shoals, central Great Barrier Reef, Australia. *Coral Reefs* 22, 499–505. <https://link.springer.com/article/10.1007/s00338-003-0344-z>.
- Soares, M.O., Teixeira, C.E.P., Ferreira, S.M.C., Gurgel, A.L.A.R., Paiva, B.P., Menezes, M. O.B., Davis, M., Tavares, T.C.L., 2019a. Thermal stress and tropical reefs: mass coral bleaching in a stable temperature environment? *Mar. Biodivers.* <https://link.springer.com/article/10.1007/s12526-019-00994-4>.
- Soares, M.O., Rossi, S., Gurgel, A., Lucas, C.C., Ferreira, S.M.C., Tavares, T.T.C., Diniz, B., Feitosa, C., Rabelo, E., Pereira, P.H., Kikuchi, R.K.P., Leão, Z.M.A.N., Cruz, I., Alvarez-Filip, L., Global and local impacts on marginal coral reefs (SW Atlantic). *Coral Reefs*. submitted, (under review). Submitted for publication.
- Soares, M.O., Tavares, T., Carneiro, P.B.M., 2019b. Mesophotic ecosystems: distribution, human impacts, and conservation in the South Atlantic. *Divers. Distrib.* 25 (2), 255–268. <https://doi.org/10.1111/ddi.12846>.
- Suzuki, G., Keshavmurthy, S., Hayashibara, T., Wallace, C.C., Shirayama, Y., Chen, C.A., Fukami, H., 2016. Genetic evidence of peripheral isolation and low diversity in marginal populations of the *Acropora hyacinthinus* complex. *Coral Reefs* 35 (4), 1419–1432. <https://link.springer.com/article/10.1007/s00338-016-1484-2>.
- Teixeira, C.D., Leitão, R.L.L., Ribeiro, F.V., Moraes, F.C., Neves, L.M., Bastos, A.C., Pereira-Filho, G.H., Kampel, M., Salomon, P.S., Sá, J.A., Falsarella, L.N., Amario, M., Abieri, M.L., Peireira, R.C., Amado-Filho, G.M., Moura, R.L., 2019. Sustained mass coral bleaching (2016–2017) in Brazilian turbid-zone reefs: taxonomic, cross-shelf and habitat-related trends. *Coral Reefs* 1, 1–13. <https://link.springer.com/article/10.1007/s00338-019-01789-6>.
- Wang, L., Shantz, A.A., Payet, J.P., Sharpton, T.J., Foster, A., Burkepile, D.E., Thurber, R. V., 2018. Corals and their microbiomes are differentially affected by exposure to

- elevated nutrientes. *Front. Mar. Sci.* 5, 101. <https://www.frontiersin.org/articles/10.3389/fmars.2018.00101/full>.
- Woesik, R.V., Sakai, K., Ganase, A., Loya, Y., 2011. Revisiting the winners and losers a decade after coral bleaching. *Mar. Ecol. Prog. Ser.* 434, 67–76. <https://doi.org/10.3354/meps09203>.
- Wong, J.S.Y., Chan, Y.K.S., Lionel Ng, C.S., Tun, K.P.P., Darling, E.S., Huang, D., 2018. Comparing patterns of taxonomic, functional and phylogenetic diversity in reef coral communities. *Coral Reefs* 37 (3), 737–750. <https://link.springer.com/article/10.1007/s00338-018-1698-6>.