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Advancing conservation planning for persistence: design of a conservation strategy for Brazilian coral reefs

Thesis submitted by

Rafael Almeida Magris (M. Sc.) James Cook University

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Statement on the contribution of others

Nature of Assistance	Contribution	Names, Titles (if relevant) and Affiliations of Co-Contributors
Intellectual support	Supervision	Prof Robert Leslie Pressey[1]
	Co-supervision	Prof Andrew Baird[1] Dr Rebecca Weeks[1]
	Editorial assistance	Prof Robert Leslie Pressey[1] (whole thesis) Dr Rebecca Weeks[1] (Chapters 1, 3, 4 and 7) Dr Morena Mills[2] (Chapters 2 and 6) Dr Mariana M.P.B. Fuentes[3] (Chapter 2) Dr Eric A. Treml[4] (Chapter 4) Dr Scott F. Heron[5] (Chapter 5) Dr Natalie C. Ban[6] (Chapter 3)
	Modelling assistance	Dr Eric A. Treml[4] (Chapter 4) Dr Scott F. Heron[5] (Chapter 5)
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[1] ARC Centre of Excellence for Coral Reefs Studies, James Cook University, Queensland 4814, Australia

[2] Global Change Institute, University of Queensland, Brisbane, Queensland 4072, Australia

[3] Earth, Ocean and Atmospheric Science, Florida State University, Tallahassee, Florida 32306-4320, USA

[4] School of BioSciences, University of Melbourne, Melbourne, Victoria 3010, Australia

[5] National Oceanic & Atmospheric Administration Coral Reef Watch, Townsville, Queensland, Australia; Physics Department, Marine Geophysical Laboratory, College of Science, Technology and Engineering, James Cook University, Townsville, Queensland 4814, Australia

[6] School of Environmental Studies, University of Victoria, Victoria, British Columbia V8W 3R4, Canada

[7] Departament of Ecology and Zoology, Federal University of Santa Catarina, Florianopolis, Santa Catarina 88010970, Brazil

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Abstract

Multiple stressors threaten coral reefs globally, causing severe declines of biodiversity and detrimental changes in the provision of associated ecosystem services. To counteract the ongoing biodiversity loss, systematic conservation planning provides a powerful framework to foster conservation and optimise allocation of conservation resources. However, conservation planning in the marine realm has focused mostly on representation of static elements of biodiversity within a system of marine protected areas (MPAs). The general failure of conservation planning to directly address persistence might impair the effectiveness of conservation plans. To ensure the efficacy of MPAs for future benefit, conservation planning must be capable of addressing ecological processes amenable to spatial management and mitigating threats to the long-term maintenance of biodiversity.

The overarching objective of my thesis is to enhance the procedures by which conservation features related to processes - those both promoting and threatening the persistence of biodiversity - can be incorporated into MPA design. To enhance this integration, I focus on two influences on biological persistence, which are particularly important for fostering coral-reef conservation, but not yet well developed and interpreted in terms of conservation planning: connectivity and climate warming. By using Brazilian coral reefs as a case study, I developed methodological approaches to MPA network design that improve upon previous approaches to marine conservation for persistence in several ways: (i) by demonstrating how to formulate conservation objectives to specifically address connectivity and climate warming (Chapters 2-5); (ii) by interpreting and combining modelling tools with MPA network design that help make conservation planning more

effective in addressing processes (Chapters 4 and 5); and (iii) by showing the value of setting these conservation objectives from the outset of planning (Chapter 6).

I first quantified the spatial extent of Brazilian MPAs to protect coral reefs and investigated their spatial and geographic attributes (Chapter 2). Based on the bias in the distribution of MPAs, my study highlights that a systematic expansion of MPAs in Brazil is urgently needed to move toward an ecologically representative and functioning MPA system. Because I interpreted principles of connectivity and climate warming through generic design criteria, I next investigated more specific and tailored recommendations to formulate better conservation requirements for persistence (Chapter 3). By reviewing the conservation literature, I outlined a framework for setting marine conservation planning objectives. The framework describes six key approaches to more effectively integrating connectivity and climate warming into conservation plans, aligning opportunities and minimizing trade-offs between both goals.

Building on this framework, I then developed methodological approaches that could be taken by planners to inform more effective planning with respect to connectivity and climate warming. In Chapter 4, I showed how functional demographic connectivity for four reef-associated species with varying dispersal abilities and a suite of connectivity metrics weighted by habitat quality can be used to set conservation objectives and inform MPA placement. Similarly, I developed an MPA design approach in Chapter 5 that includes spatially- and temporally-varying sea-surface temperature data, integrating both observed and projected time-series, to derive quantitative objectives for thermal-stress regimes.

In Chapter 6, I re-examined the performance of Brazilian MPAs to achieve a well-balanced set of conservation objectives, explored interactions between different sets of objectives, and evaluated the consequences of pursuing single sets objectives separately in

marine planning. Despite large spatial extent of MPAs protecting Brazilian coral reefs, I found the existing MPAs are placed in sub-optimal locations, unable to accumulate larvae, to function as migratory pathways, and to promote resilience to warming disturbances.

Overall, my thesis demonstrates that stronger methodological frameworks can operationalize marine conservation planning for ecological connectivity and climate warming, resulting in improved conservation outcomes in the sea. The key requirement for this incorporation is to formulate quantitative conservation objectives underpinned by ecologically-informed parameters in the initial stages of planning.

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Chapter 1. General introduction

Coral reefs are considered to be the most biologically diverse and productive ecosystems on the planet (Hoegh-Guldberg et al. 2007). They are essential components of tropical coastal seascapes, and provide important ecosystem services including production of harvested species, structural coastal protection, nutrient cycling, medicines, ornaments and recreational opportunities (Moberg and Rönnbäck 2003). Globally, coral reefs cover about 527,000 km^2 (Mora et al. 2006), but in recent decades many reefs have come under intense human pressure, with world coral-reef coverage decreasing by approximately 20%, with an additional 20% under serious degradation (Millennium Ecosystem Assessment 2005).

The potential for coral reefs to contribute economically and through provision of ecosystem services is threatened by the exposure of reefs to multiple stressors that lead to cumulative impacts (Hoegh-Guldberg et al. 2007). Here, I use ‗stressor‘ to refer to an environmental variable that has a deleterious effect on coral reefs (i.e. a disturbance). The stressors stem from a multiplicity of causes. Stressors with local causes include overfishing and increased eutrophication, which can be mitigated directly by managers. Stressors with global causes, such as global warming and ocean acidification, cannot be directly addressed by managers, although their effects can be mitigated by local management (Bellwood et al. 2004; Hughes et al. 2003). The dramatic degradation of coral reefs necessitates rational, accountable, cost-effective conservation management to counteract both types of stressors. This is particularly important in developing countries where high dependence on marine resources creates strong competition between short-term social and commercial interests and longer-term concern for environmental conservation (Dahdouh-Guebas 2002).

1.1 Conservation planning for coral reefs

Marine protected areas (MPAs) are increasingly viewed as an important spatial management tool within a suite of policy alternatives to address rapid declines in coral reef biodiversity (Mumby and Steneck 2008). This has led to a global proliferation of MPAs to protect coral reefs (Mora et al. 2006). The establishment of an array of individual MPAs within a particular study area can encompass a wide range of management types and levels of protection. If an MPA system is intended to be ecologically connected, it can form an MPA network. Where properly implemented, MPA networks have proven to be effective tools for reef conservation, with documented empirical evidence of their benefits (Harrison et al. 2012; Mumby and Harborne 2010; Olds et al. 2013). However, uncertainty remains over strategies to optimize MPA spatial design, placement, and evaluation for the protection of biodiversity *in situ* and ecosystem resilience (Claudet et al. 2008; McCook et al. 2010). Optimising the design and implementation of MPA networks is a central concern of marine spatial planning.

The need to improve MPA network design has led to an important paradigm shift from *ad hoc* reserve establishment to systematic conservation planning (Margules and Pressey 2000), whereby a combination of methods and scientific approaches can facilitate and contribute to optimal reserve design (Kati et al. 2004; Pressey 1994; Sarkar et al. 2006). The key foundation of these multistep procedures is the emphasis on meeting quantitative conservation objectives within an explicit, transparent decision-making framework (Margules and Pressey 2000). In this context, many methods utilise site selection and decision-support algorithms to provide decision-makers with guidance and the flexibility to explore spatial options when proposing MPA networks (Pressey and Bottrill 2009).

Currently, the core consideration underpinning the use of such support tools and MPA design relate to the principle of maximising biogeographic representation and habitat heterogeneity within

MPAs, while minimising socioeconomic costs incurred during their implementation (Moilanen 2008; Pressey et al. 1993; Sarkar et al. 2006). However, given that encompassing a representative sample of biodiversity might not ensure the persistence of natural features through time (Halpern and Warner 2003; Margules and Pressey 2000), effective conservation planning must be capable of addressing ecological processes amenable to spatial management and mitigating threats to the long-term maintenance of biodiversity. Yet, formulation and integration of such processes is often overlooked in conservation planning (Cabeza and Moilanen 2001; Pressey et al. 2007). Clearly, improving MPA design for persistence, complementing the longstanding focus on biodiversity representation, is essential to ensure adequate protection of coral-reef systems over the next century.

In my thesis, I seek to address two influences on persistence, which are particularly important for fostering coral-reef conservation, but not yet well developed and interpreted in terms of conservation planning: connectivity and climate warming.

1.2 Connectivity and coral-reef conservation

The spatial arrangement of habitat patches and the physical linkages among them are key determinants of the distribution, movement, growth, and survival of coral reef organisms (Jones et al. 2009). Most reef-associated species perform juvenile or adult migrations or have a highly dispersive larval phase, which results in an exchange of individuals between natal and non-natal sites (Green et al. 2014b). This connectivity is central to the dynamics of population viability and the maintenance of the underlying patterns of biological diversity and community structure. Indeed, connectivity is vital for a wide range of ecological and evolutionary processes, including population replenishment and maintenance of genetic diversity, which underpin population persistence and resilience (Foley et al. 2010; Jones et al. 2009; Jones et al. 2005). Maintenance of connectivity is therefore of key importance for maintaining fisheries and other goods and services provided by coral-reef ecosystems

(McCook et al. 2009). Concerningly, coral reefs are being increasingly fragmented by coastal development and connections are being weakened through the wholesale removal of mobile organisms or severe depletion of populations (Hughes et al. 2005; Jones et al. 2009).

1.3 Climate change and coral-reef conservation

In addition to ecological connectivity, maximizing the persistence of coral-reef biodiversity requires planning that considers broad-scale processes such as ocean warming (Mumby et al. 2011). Coral reefs are among the earliest ecosystems to show marked ecological responses to climate warming (Hoegh-Guldberg et al. 2007), and such sensitivity increases the extinction risk for many species (Pratchett et al. 2008). Warming disturbances on coral reefs are expected to include reduced coral growth (McClanahan et al. 2012), decreased capacity to recover from a suite of other stressors (Hoegh-Guldberg et al. 2007), mass coral mortality associated with bleaching events (Baker et al. 2008), shifts in species ranges (Makino et al. 2014b), and coral disease outbreaks (Bruno et al. 2007). The mechanisms controlling larval dispersal and their relationships with environmental conditions are also sensitive to climate change (Munday et al., 2009). All these broad-scale changes affect entire coral reef ecosystems, resulting in declines in biodiversity, fisheries yield, and other ecosystem services. Global warming causes reef decline even where reefs are well managed or remote from other human stressors (Hughes et al. 2003). Consequently, pragmatic conservation actions are required to address new challenges to conserving coral-reef systems in face of unprecedented and unstoppable sea-temperature warming.

1.4 Brazilian coral reefs

The northeast coast of Brazil is home to the only true coral-reef ecosystems in the South Atlantic (Leão and Dominguez 2000). Brazilian coral reefs are considered a conservation priority in the southwestern Atlantic Ocean as they have high species endemism, harbour many threatened species, and form structures significantly different from the well-known coral-reef ecosystems of the Caribbean and Indo-Pacific regions (Bender et al. 2013; Castro and Pires 2001; Francini-Filho and de Moura 2008; Leão and Dominguez 2000). Hotspots of endemism have been identified in shelf-edge reefs located in eastern and north-eastern Brazilian waters (Olavo et al. 2011) and the Abrolhos Bank (Leão and Dominguez 2000).

The spatial distribution of Brazilian reefs is marked by geographical discontinuities, which appear to be delineated by low-salinity barriers to the exchange of individuals (Nunes et al. 2009). The degree of connectivity between these separated populations is of interest because it provides insight into processes at both evolutionary and ecological time scales, such as persistence of reef-associated species. Although studies have explored the permeability of the salinity barriers to gene flow between distantly separated populations along the Brazilian coast (Floeter et al. 2008; Floeter et al. 2001), there is a lack of studies measuring species-specific demographic dispersal and the biophysical drivers of marine population connectivity.

The magnitude of human disturbances on Brazilian coral reefs necessitates increased efforts for the conservation of these unique and fragile ecosystems (Barreira e Castro et al. 2012; Freitas et al. 2011; Miranda et al. 2013). Although Brazilian reefs appear to conform only partially with global patterns of bleaching (Leão et al. 2008) and contain scleractinian coral communities with enhanced capabilities for surviving acute events (Kelmo et al. 2003), warming temperatures appear to be associated with both coral bleaching (Leão et al. 2010b) and the incidence of coral diseases (Francini-Filho et al. 2008).

1.5 Thesis objectives and structure

The overarching objective of my PhD project is to advance conservation planning for biological persistence by improving the integration of ecological connectivity and climate warming into the design of marine protected areas. Despite the rise of studies acknowledging the importance of planning for connectivity (Almany et al. 2009; Fox et al. 2011; Green et al. 2014b; Treml and Halpin 2012) and climate change (Chollett et al. 2014; Game et al. 2008b; McLeod et al. 2012; Mumby et al. 2011), these processes are yet to be comprehensively incorporated into a coherent framework. My thesis addresses this critical gap, facilitates the inclusion of ecological connectivity and climate warming into future conservation planning exercises, and provides a framework for an informed decision-making process.

The key specific objectives of the thesis are to:

1. evaluate progress made by MPAs in Brazil towards meeting conservation objectives regarding representation and persistence, and provide an overview of the conservation status of Brazilian marine ecosystems, including coral reefs (Chapter 2).

> Setting conservation objectives is an important step in systematic conservation planning and shapes subsequent steps in planning. Evaluations of performance and accomplishment of MPAs have been mostly addressed through formulation of objectives with respect to representation. In Chapter 2, I interpret principles of connectivity and risk spreading to assess if / how well existing MPAs meet specific spatial configuration criteria related to persistence while also representing broadly defined marine ecosystems. In this chapter, I outline the biases and discrepancies in the spatial distribution of MPAs in Brazil. I also discuss the need to expand the existing system of MPAs in Brazil and ways to make the required expansion more ecologically effective.

2. explore how well ecological connectivity and climate-warming effects have been incorporated into marine conservation planning, and propose ways forward that enhance their integration (Chapter 3);

Chapter 3 presents the most updated and comprehensive database collated to identify ecologically relevant ways of setting conservation objectives regarding persistence in relation to connectivity and climate warming. By reviewing 134 peer-reviewed studies and reports, I provide and discuss a framework that increases the accessibility of evidence to support more effective decision-making processes. I also outline strategies that might create trade-offs between objectives for connectivity and climate change and the opportunities to align their concurrent achievement. This chapter provides a foundation for fully developing methods that would refine conservation planning with respect to persistence.

3. develop new approaches for integrating ecological connectivity and climate warming into conservation planning for coral reefs, and demonstrate the formulation of conservation objectives that explicitly account for these processes (Chapters 4 and 5);

Building on the framework provided by Chapter 3, I developed novel approaches to improve integration of ecological connectivity and climate warming into marine reserve design (Chapters 4 and 5, respectively). In Chapter 4, biophysical modelling is combined with remote-sensing techniques to identify spatial patterns in large-scale connectivity of reef-associated species and assess the influence of threating processes on those patterns. This is the first attempt to include multiple-species connectivity into decision-support tools to inform MPA placement and the first study to determine whether combined connectivity data from species with varying dispersal abilities are effective surrogates for individual species. Implications of using a holistic analytical approach to tackle issues relevant to planning for connectivity are discussed. Chapter 5 presents an approach to incorporate climate-warming disturbances in conservation planning to design climatically representative coral-reef MPAs. This integration is improved by demonstrating how to spatially configure MPAs that meet conservation objectives for climate resilience using spatially- and temporally-explicit data, and by strategically allocating different forms of spatial management (MPA types) intended to mitigate climate-warming disturbances.

4. explore potential synergies between conservation objectives for biodiversity, connectivity, and climate warming, and demonstrate the benefits of their systematic integration when designing network of MPAs (Chapter 6).

Chapter 6 deals with possible interactions between conservation objectives for biodiversity, connectivity, and climate warming. I combine findings from the previous Chapters 4 and 5 to refine the conservation objectives formulated in Chapter 2. The refined conservation objectives for biodiversity are reformulated with information on a finer delineation of coral-reef ecosystems, functional biological diversity, dispersal patterns of reef-associated species, and spatial and temporal patterns of warming disturbance. By performing a more nuanced gap analysis, I re-examine the performance of existing MPAs for coral reefs and analyse the misfit between them and priority areas that strategically achieve a well-balanced set of conservation objectives. Finally, I evaluate some implications of pursuing a systematic expansion of MPAs to achieve multiple objectives that would reduce the current shortfalls.

Apart from this general introduction (Chapter 1), the thesis proceeds as a progression of five independent data chapters (Chapter 2 through 6), formatted as peer-reviewed manuscripts, whose findings are integrated to yield recommendations for biodiversity management, which are highlighted in a general discussion (Chapter 7). In Chapter 7, I also present some ideas and discuss research gaps for future development of research in this area. Although I use Brazilian reefs as a case study, the models developed here are generally applicable elsewhere.

Chapter 2. Analysis of progress towards a comprehensive system of marine protected areas in Brazil[1]

Abstract

Brazilian marine ecosystems face great threats while retaining outstanding biological features. A gap analysis was conducted to evaluate how well MPAs in Brazil meet conservation objectives for representation, connectivity, and risk-spreading. The performance of the MPAs was evaluated by overlaying maps of ecosystem and management and calculating the size of no-take areas and the distances between them. All objectives were far from fully attained. Currently, the protection of the marine environment is poor, with less than 1.9% of Brazil‘s marine jurisdiction within MPAs and 0.14% within no-take areas. Also, only 23% of the ecosystems met the minimal number of replicates required by the risk-spreading objective. More positively, just over half (51%) of the no-take areas are a desirable distance apart. My study highlights that a systematic expansion of MPAs in Brazil is urgently needed to move toward an ecologically representative and functioning MPA system.

2.1 Introduction

Marine ecosystems are experiencing accelerating and alarming ecological degradation and loss of species, both of which impair the ocean‘s capacity to provide food, maintain water quality,

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and recover from perturbations (Worm et al. 2006). Declines of marine species and degradation of ecosystems have occurred primarily as a result of over-harvesting, pollution, and the large-scale disturbances of climate change (Halpern et al. 2008). Similar to the global situation, Brazilian marine ecosystems and species are subject to many human-imposed stressors, with coastal waters and estuaries adjacent to the Brazilian coast experiencing increased pressures (Halpern et al. 2012; Halpern et al. 2008).

The outstanding biological features of the Brazilian marine environment (e.g. Leão and Dominguez (2000)), coupled with expanding and intensifying threats to marine biodiversity, highlight the need for conservation management and promotion of sustainable use of biodiversity. Important tools for both conservation and sustainable use are MPAs. Protected areas are designated or regulated, and managed to achieve specific conservation objectives (CBD 2013). As a commitment to reducing declines in marine biodiversity, Brazil has signed and ratified the Convention on Biological Diversity (CBD). More recently, Brazil has agreed to achieve the Aichi Biodiversity Targets, with a goal of encompassing 10% of its seas and coastal areas within an effectively managed, ecologically representative and well connected MPA network by 2020 (CBD 2013). In addition, the Brazilian government committed to implement the National Protected Areas Plan, with the overall goal of consolidating a system of effectively managed and ecologically representative protected areas by 2015 (Brasil 2006). However, only a small portion (1.87%) of Brazil‘s marine jurisdiction is currently under protection. Therefore, an expansion of the MPA system in Brazil, systematically designed to maximize the benefits for biodiversity, is timely.

Systematic conservation planning provides a valuable framework for MPA network design, using quantitative objectives to guide the configuration of protected areas to promote the representation and persistence of biodiversity *in situ* (Pressey et al. 2007). Representation of species (biodiversity pattern) can be obtained by selecting protected areas that sample the biotic diversity of the marine ecosystems with which they are associated (Harris and Whiteway 2009). Planning for persistence is less evolved (Pressey et al. 2007) because it requires that biodiversity processes are conserved, directs attention to dynamic threats, and demands more data than when planning for representation. To overcome the existing lack of data to plan for persistence, generic design criteria have been developed with the aim of minimizing disturbances from stressors to ecosystems, promoting connectivity between populations, and supporting other important processes (e.g. Airamé et al. (2003), Fernandes et al. (2005), Green et al. (2009)).

A key step in conservation planning is a gap analysis (Rodrigues et al. 2004; Spalding et al. 2008), in which the achievement by protected areas of quantitative objectives for representation and persistence is reviewed (Pressey et al. 2007). This helps identify areas, species and ecosystems that require further protection. To guide future ecologically effective expansion of MPAs in Brazil, I undertake a marine gap analysis to assess how well Brazil meets conservation objectives for representation and persistence.

2.2 Materials and Methods

A gap analysis (Fig. 2.1) was undertaken to determine how well conservation objectives were met by the existing MPAs in the entire oceanic area under Brazilian national jurisdiction (Exclusive Economic Zone – EEZ; 3,642,070 km^2, Fig. S1). The gap analysis involved interpreting three principles – representation, connectivity, and risk spreading - into explicit conservation objectives and assessing the performance of the current system of marine protected areas in achieving these objectives (see Section Gap Analysis).

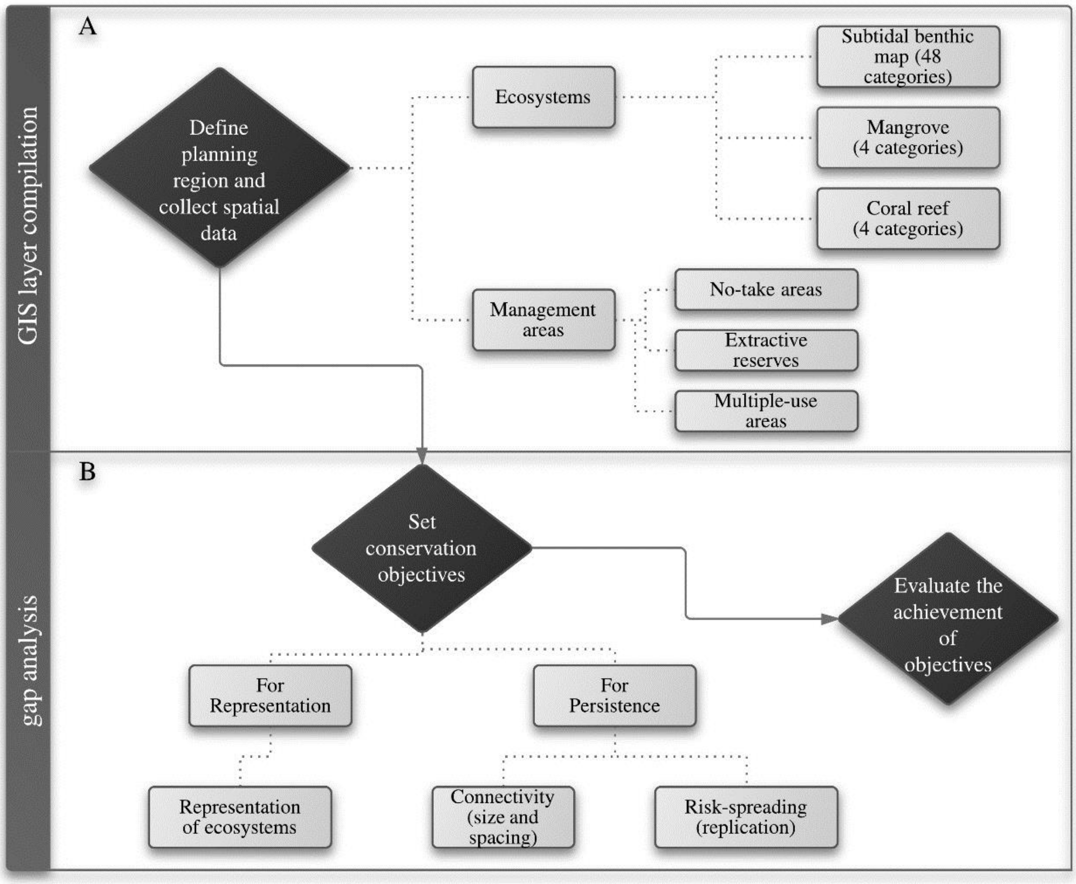

Figure 2.1 Schematic flowchart depicting all steps in the methods for this chapter, including the two broad phases: GIS layer compilation (A) and gap analysis (B). The main groups of steps are indicated by dark diamonds. Light boxes show steps and types of data or objectives extracted or derived.

2.2.1 Geographic Information System (GIS) layer compilation

All available ecosystem and marine resource management maps were compiled (Fig. 2.1A), using ArcGIS v10 software. Ecosystems included: coral reef, mangrove, and other substrata in six depth zones: 0-10m, 10-25m, 25-50m, 50-75m, 75-100m, and >100m). These were intersected with eight ecoregions - 1. Amazon; 2. Northeastern; 3. Eastern; 4. Fernando de Noronha and Atoll das Rocas; 5. São Pedro and São Paulo Islands; 6. Trindade and Martin Vaz Islands; 7. Southeastern Brazil; and 8. Rio Grande - to produce 56 ecosystems. Further details about the ecosystem map are in Appendix C2. This was the best available national delineation of marine ecosystems. Other ecosystems could have been chosen in light of their biological relevance for marine species (*e.g.* rocky reef, seagrass), but their distributions were not available for the entire Brazilian marine jurisdiction at reasonable accuracy. Conservation assessment based on broad ecosystems (such as bioregions and depth classes) are often necessary due to lack of knowledge about the distributions of more finely subdivided ecosystems and their associated species (Lombard et al. 2007; Mills et al. 2011).

Information on location of MPAs in Brazil was gathered and compiled from datasets held by the Brazilian Ministry of Environment and other environmental organizations (e.g. http://www.mma.gov.br/areas-protegidas/cadastro-nacional-de-ucs). This spatial dataset consisted of 142 MPAs under three levels of governance: federal, state, and municipal. MPAs were considered as those areas with estuarine or oceanic biota, including all MPAs that intersected the upper intertidal zone (upper limit of occurrence of mangrove ecosystems). MPAs were placed into three broad categories with different forms of management intent: no-take areas, extractive reserves, and multiple-use areas. The main characteristics of each category are described in Appendix C2. This was necessary because Brazilian MPAs embrace a wide range of management types (Brasil 2000). The ―management" dataset encompassed the legal boundaries of 56 no-take areas, 23 extractive reserves, and 63 multiple-use areas.

2.2.2 Gap Analysis

Having compiled maps of ecosystems and MPA types, I conducted a gap analysis to assess the extent to which the conservation objectives for representation and persistence had been achieved (Fig. 2.1B). Objectives for representation were percentages of each ecosystem type (Rondinini and Chiozza 2010). Objectives for persistence (Pressey et al. 2007) related to connectivity and risk spreading.

The representation objectives were 30% coverage of each ecosystem within the MPA system and 20% coverage of each ecosystem within no-take areas. These objectives can be refined according to various criteria (e.g. Pressey et al. (2003)) and should be seen by conservation practitioners as temporary measures whilst objective-setting based on species-area relationships (Metcalfe et al. 2013), rarity, threats and other criteria is underway. The 30% target is the “average percentage of protected area recommended as necessary to conserve various aspects of biodiversity” for evidence-based conservation assessments (Svancara et al. 2005). The no-take area target is based on studies suggesting that, for fisheries management and to prevent major loss of species richness, no-take areas need to cover at least 20% of the extent of each marine ecosystem (Beck and Odaya 2001; Fernandes et al. 2005). Although the Brazilian Government has committed to achieving the Aichi Biodiversity Targets, the representation objective should not be constrained by the Aichi percentage of 10%, which is a policy-driven target without consideration of ecological requirements (Svancara et al. 2005).

For connectivity, I stipulated that a single no-take area should have a minimum size of 10 km^2 and the distance between adjacent no-take areas should not exceed 15 km (Green et al. 2009; Halpern and Warner 2003; Shanks et al. 2003). I focused on these aspects of design because they are often suggested as critical considerations to maintain connectivity between populations (Roberts et al. 2003). The application of size and spacing thresholds only to no-take areas was intended to ensure strong connectivity given uncertainty around the effectiveness of extractive reserves and multiple-use areas for biodiversity conservation and the desirable configuration of these other MPA types (CBD 2013). The rules of thumb for connectivity can also be refined when more information is available on larval dispersal (Almany et al. 2009) and adult movements (Kramer and Chapman 1999) for species of interest.

The risk-spreading objective was at least three examples of each ecosystem type in the same ecoregion in different no-take areas (Green et al. 2009). Replication of conservation features across multiple no-take areas lessens the probability that a catastrophic event (e.g. oil spill, mass bleaching) within a no-take area will eliminate entire protected populations of species (Airamé et al. 2003; Roberts et al. 2003). Objectives for risk-spreading took into account only no-take areas as a precautionary approach. Data to measure the susceptibility to disturbances of species and ecosystems, combined with effects of extractive uses, are unavailable for extractive reserves and multiple-use areas. These objectives can be refined for subsequent gap analyses with information on the spatial and temporal patterns of disturbances (Allison et al. 2003; Ban et al. 2012), species responses, and recovery rates in different kinds of MPAs.

The ecosystem map was overlaid with a data layer containing management area boundaries to identify gaps in coverage and quantify the extent to which representativeness and risk-spreading objectives had been achieved by the existing MPAs. Wherever MPA boundaries overlapped, I recognised the most restrictive management category (no-take area > extractive reserve > multiple-use areas). For connectivity, I calculated the size of each single no-take MPA and the Euclidean distance between nearest pairs of centroids of no-take MPAs. If no-take areas contained spatially separate sections, I examined each polygon individually (56 no-take areas resulted in 91 individual polygons). All analyses were performed using ArcGIS v10.

2.3 Results

2.3.1 Representation

MPAs covered 192,343 km^2 (1.87%) of the waters within the Brazilian EEZ, although only 0.14% was within no-take areas. The representation objectives were far from being fully attained.

Most (>85%) of the ecosystems fell short of having 20% coverage by no-take areas (Fig. 2.2), with median coverage by no-takes at 0.01% (mean coverage of 11%). There were also substantial shortfalls in achieving the 30% objective for coverage by all MPA categories. Only 26% of ecosystems met this objective (Fig. 2.2) with median coverage by all MPAs at 1.31% (mean coverage of 21%).

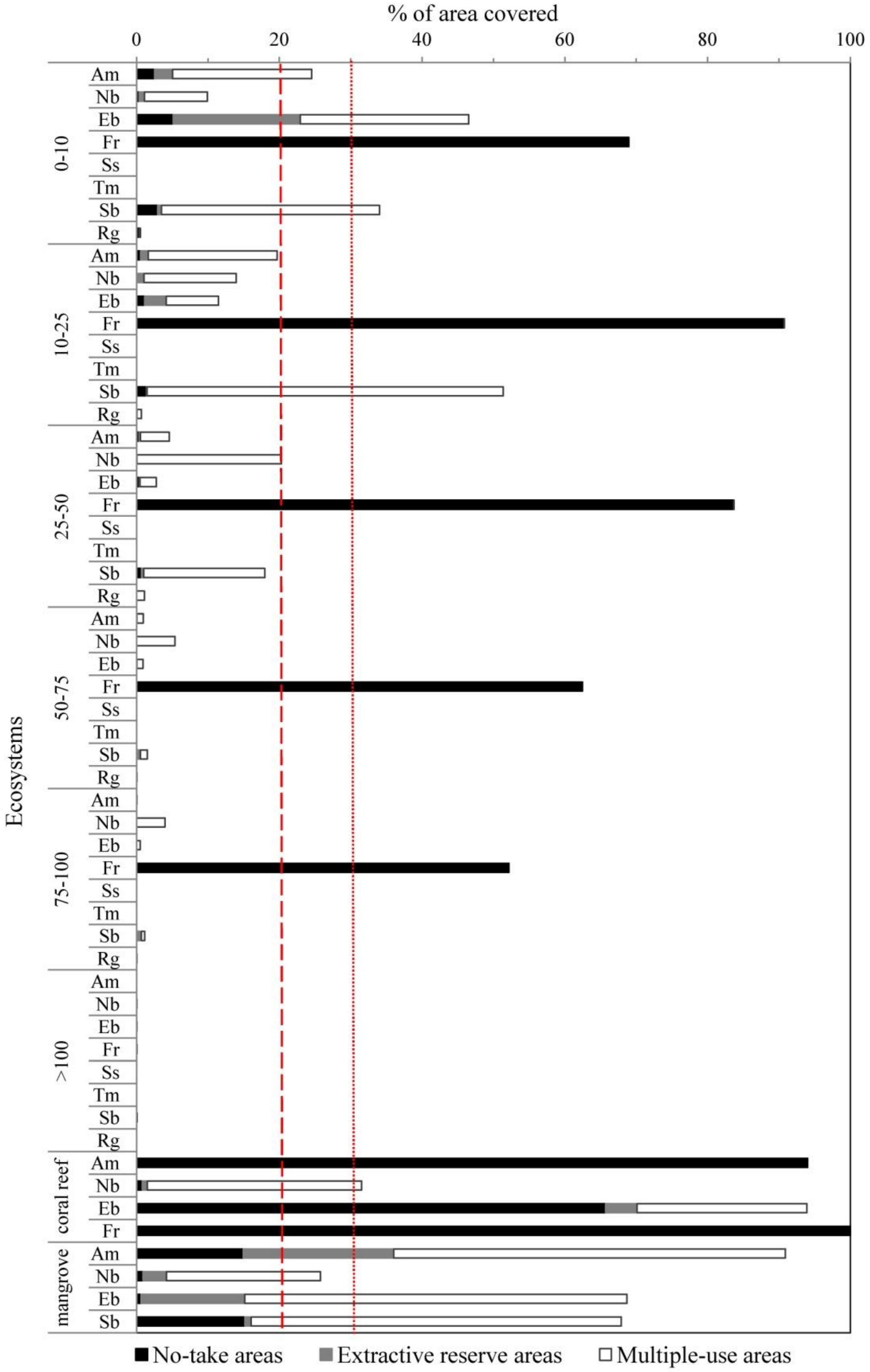

Figure 2.2 Percentage of each ecosystem covered by the three types of MPAs. Abbreviations for ecoregions: Am=Amazon, Nb=Northeastern Brazil, Eb= Eastern Brazil, Fr= Fernando de Noronha and Atoll das Rocas, Ss= São Pedro and São Paulo Islands, Tm= Trindade and Martin Vaz Islands, Sb=Southeastern Brazil, Rg=Rio Grande. Thicker red dashed vertical line indicates our 20% objective for representation in no-take areas. The other vertical line indicates our 30% objective for all MPA categories.

Twenty-five percent of ecosystems had no coverage by all MPAs combined, and 50% had no coverage by no-take areas. Only coral reefs and ecosystems in one ecoregion (Fernando de Noronha and Atoll das Rocas) were adequately protected according to the objectives. Under-protected ecosystems were distributed throughout the Brazilian EEZ but protection was consistently poor for ecosystems deeper than 100m, the oceanic ecoregions São Pedro and São Paulo Islands and Trindade and Martin Vaz Islands, and the Rio Grande ecoregion. Although mangroves in Amazon, Eastern and Southeastern Brazil achieved the objectives for all MPAs combined, they were poorly represented by no-take areas. These results reflect the bias in distribution of MPA types. Several ecoregions such as Southeastern Brazil have large percentages within MPAs, dominated strongly by extensive multiple-use areas. Other ecoregions lack protection entirely (e.g. São Pedro and São Paulo Islands and Trindade and Martin Vaz Islands). The distribution of no-take areas followed a similar pattern to that of all types of MPAs combined, with two exceptions: Northeastern Brazil had an extremely small percentage under no-take protection relative to total MPA coverage, and Fernando de Noronha and Atoll das Rocas had a large percentage of no-take areas relative to all MPAs combined.

2.3.2 Connectivity

The connectivity objective was partially met. Almost half (47%) of the no-take areas were above the minimum desirable size (Fig. 2.3A). There were many small no-take areas (< 10km^2) in the Southeastern Brazil ecoregion. In contrast, all no-take areas in the Amazon ecoregion were bigger than 10 km^2. The sizes of no-take areas varied from <0.02 km^2 to 6,573 km^2. For spacing, about half the no-take areas (51%) achieved the objective (Fig. 2.3B). Spacing between no-takes varied widely from less than 0.3 km to nearly 250 km. Their spatial distribution showed a clear contrast: a cluster of no-take areas in the Southeastern Brazil ecoregion (where more than 70% of no-take areas were separated by less than 15km), while no-take areas in the Amazonn ecoregion were more widely spaced (all more than 15 km).

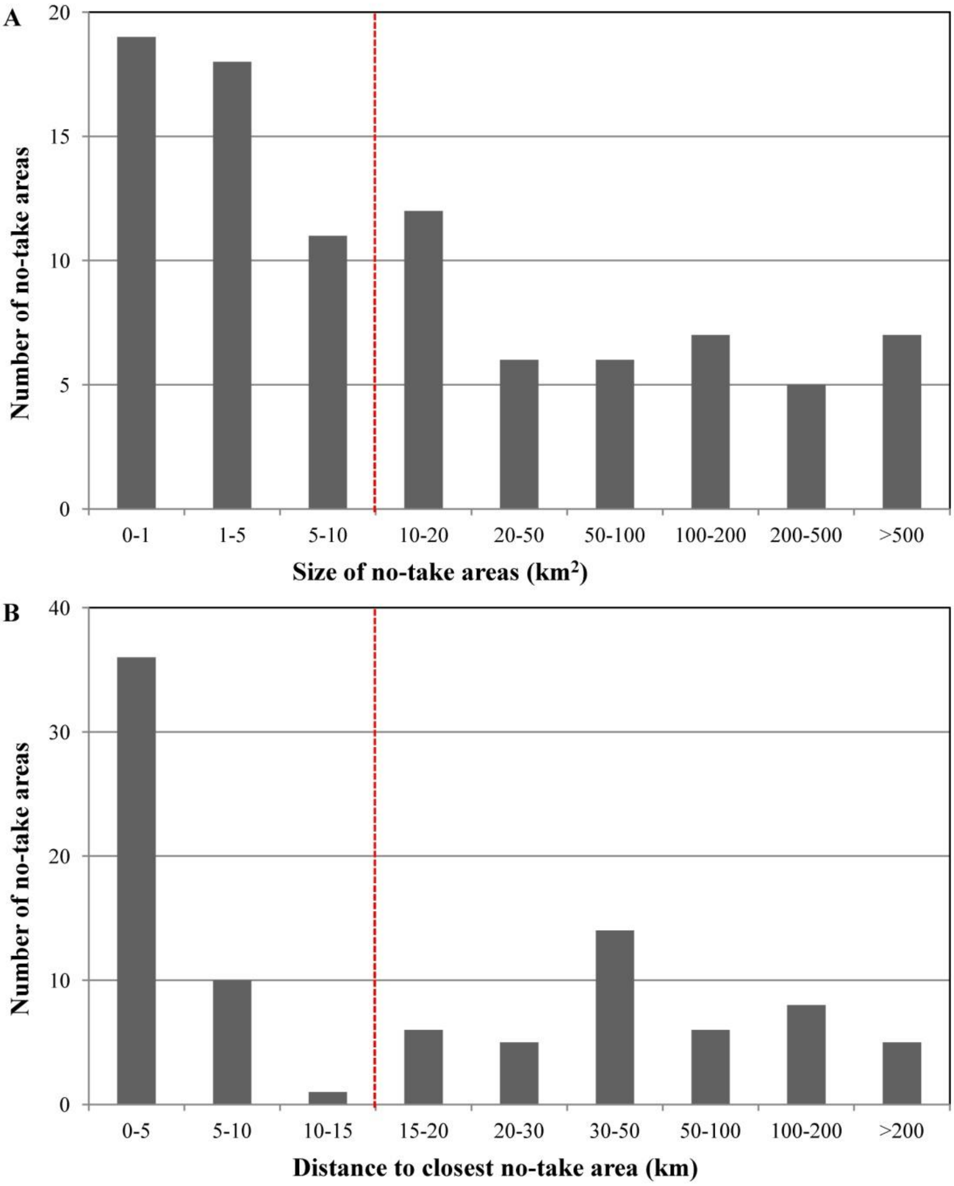

Figure 2.3 Distribution of size (A) and spacing (B) of Brazilian no-take areas. The dashed vertical red lines indicate the objectives for size (A, at least 10 km2) and spacing (B, maximum 15 km).

2.3.3 Risk spreading

Only 23% of the ecosystems met the minimal number of replicates required by the risk-spreading objective (Fig. 2.4). All ecosystems within the Southeastern Brazil ecoregion, except for those deeper than 75 m, achieved this objective. This ecoregion had 44 no-take areas protecting different shallow ecosystems between 0 and 10 meters. A shared pattern was evident in the other ecoregions: the number of replicates of shallow ecosystems inside no-take zones outnumbered those of deeper ecosystems. Some ecoregions such as Rio Grande did not achieve the replication objective for any of its ecosystems. The mangrove ecosystems were the only ones to be protected in more than 3 different no-take areas across their range. For coral reefs, no-take areas failed to achieve the risk-spreading objective in all four ecoregions in which they occurred, mainly because they were covered by few relatively large no-take areas.

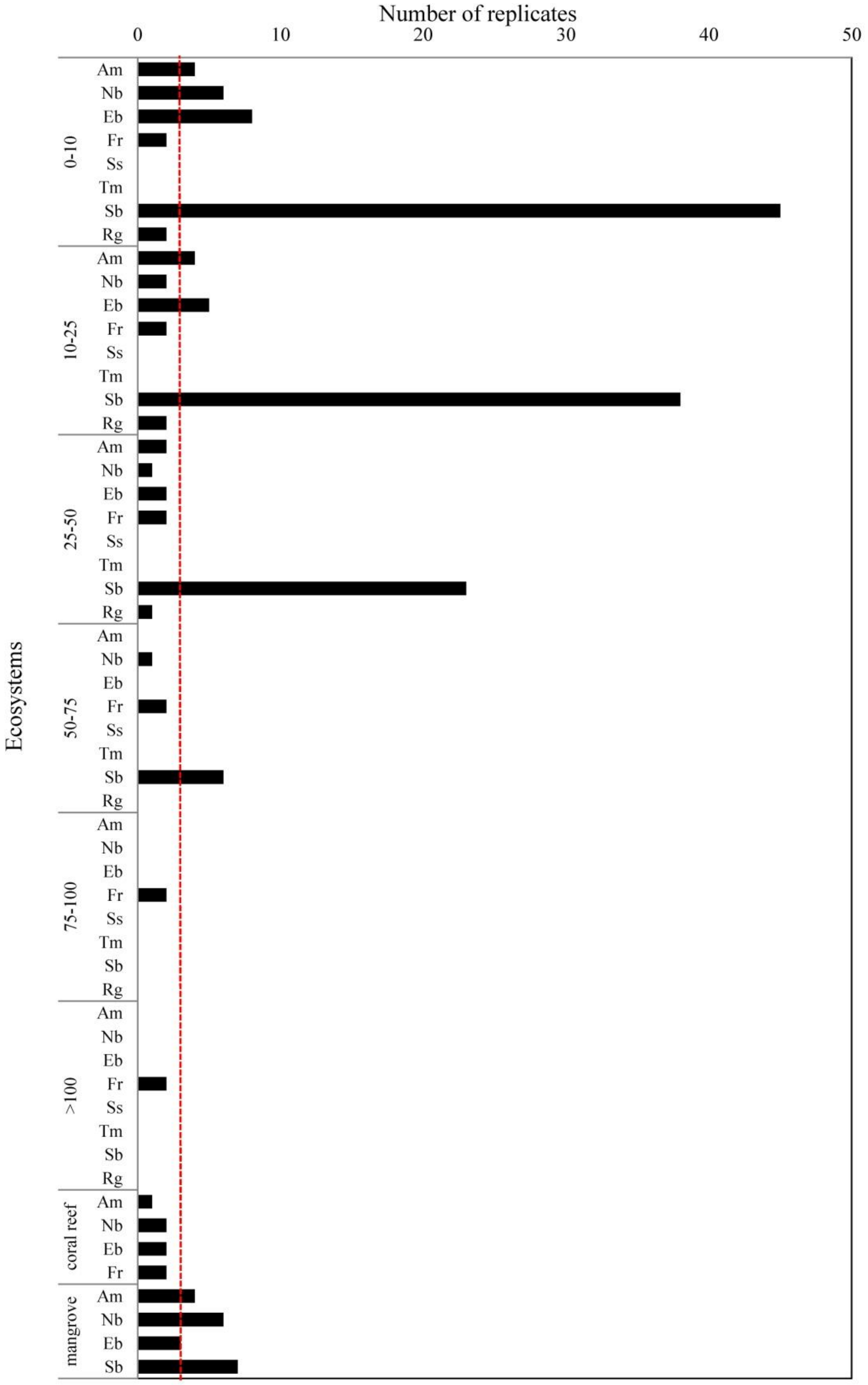

Figure 2.4 Number of replicates of each ecosystem within no-take areas. Abbreviations for ecoregional subdivisions: Am=Amazon, Nb=Northeastern Brazil, Eb= Eastern Brazil, Fr= Fernando de Noronha and Atoll das Rocas, Ss= São Pedro and São Paulo Islands, Tm= Trindade

and Martin Vaz Islands, Sb=Southeastern Brazil, Rg=Rio Grande. Red dashed vertical line indicates the conservation objective for replication.

2.4 Discussion

There is an urgent need for an increased effort to manage and protect the marine environment in Brazil to ensure its sustainability and persistence. Currently, the protection of the marine environment in Brazil is poor with less than 1.9% of the marine jurisdiction within MPAs and 0.14% within no-take areas. These figures update a recent estimate of MPA coverage from the Brazilian government (1.6% of EEZ under protection; Brasil 2010) and highlight that formal management of marine resources in Brazil is in its initial stage. This percentage coverage is much lower than the 10% national objective and the 30% best-practice recommendation for all types of MPAs (Beck and Odaya 2001; Fernandes et al. 2005; Svancara et al. 2005). An examination of the chronological pattern of creation of MPAs in Brazil (see Figure C2.3) revealed a slow rate of addition to the MPA system during the last 15 years, with only about 20% of total extent added during this period. If the rate since first establishment of an MPA creation is maintained, it will take another 25 years to achieve even the minimal Aichi target of 10% coverage of coastal and marine ecosystems to which the government is committed.

The spatial and geographic attributes of MPAs in Brazil are distinctly biased across ecosystems and ecoregions. Protection ranged from 0% to 100%, with 41 of 56 ecosystems still below the 30% level for all MPA categories. While the number of MPAs in Brazil is quite limited, the current spatial configuration of MPAs reflects findings from gap analyses in other regions (see Spalding et al. (2008)), especially from Latin America (e.g. Guarderas et al. (2008)). Around the world, systems of MPAs are arguably biased towards areas with considerable knowledge of the status of marine systems, least use of marine resources, and greater interest by organizations (Guarderas et al. 2008;

Weeks et al. 2010a). Therefore, the need for a shift of techniques and features of interest when planning new MPAs has still to be fully recognised if marine conservation is to be effective.

Determining optimum MPA size and spacing to ensure persistence requires biological information that is currently unavailable. Although 47% of the Brazilian no-take areas had the minimum size required to maintain connectivity and more than half the Brazilian no-take areas were closely spaced (Green et al. 2009; Halpern and Warner 2003), the overall system of MPAs cannot be considered well-connected. The current distribution of distances between no-take areas is not likely to encompass the dispersal distances of all species (Halpern and Warner 2003; Shanks et al. 2003). Additionally, most ecosystem types (77%) did not meet the risk spreading objective so existing MPA configuration is not contributing as a general strategy to ensure persistence with the aim of preventing the effects of disturbances on ecosystems (Álvarez-Romero et al. 2011). The rules for spatial design presented here should be tailored to region-specific connectivity requirements, which vary according to species composition, hydrodynamics, and disturbance history. To ensure viability of biological assemblages in the long term, spatial configuration of MPAs also needs to be complemented by their placement relative to features in the seascape that accumulate larvae, function as migratory pathways, and increase resilience against disturbances.

Without urgent action to protect Brazil‘s coastal and offshore waters, the dire situation of serious disturbances is likely to worsen with rapidly expanding and intensifying fishing pressure (Araújo and Martins 2009), pollution, conversion of coastal ecosystems to agricultural and urban areas (Copertino 2011), coastal development, and offshore mining and oil extraction (Da Silva et al. 1997). Importantly, a systematic approach is needed to counteract the emerging trend of MPAs being placed where they are most expedient politically but also least effective in mitigating threats to the marine environment (CBD 2013). Future research needs to carefully evaluate the extent to which placement of Brazilian MPAs is shaped by economic or social pressures. Both systematic additions to the

Brazilian MPA system and improvement of data on marine biodiversity can proceed in parallel. The study has shown that a coarse ecosystem delineation can provide helpful initial guidance for MPA design, but further delineation of ecosystems is desirable to more effectively account for spatial variations in marine biodiversity. As additional data are collected, subsequent gap analyses will yield further insights.

Further improvements to assessing protection status of marine ecosystems and species in Brazil are necessary. One way forward is to gather additional data that better represent the compositional patterns and key processes of marine biodiversity such as patch dynamics, oceanographic phenomena, and migration patterns (Grantham et al. 2011; Pressey et al. 2007). This would allow refined quantitative objectives, building on the beginnings presented in this study, for representation and persistence that reflect need for protection of features from current and emerging threats (Pressey et al. 2007). However, to date, knowledge of Brazilian marine biodiversity is poor and uneven (Amaral and Jablonski 2005), so conservation objectives are likewise constrained. Regardless, investment in marine protection should not be delayed until better data are collected (Pressey and Cowling 2001). Moreover, data on how well MPAs along Brazilian coast are managed or implemented are lacking (see Spalding et al. (2008)). Financial shortage and poor inter-institutional coordination of coastal and ocean governance have hampered effective implementation and management of MPAs in Brazil (Gerhardinger et al. 2011). Consequently, this study is likely overestimating existing marine protection. If the effectiveness of protected areas were taken into account, the results would definitely be even worse.

Increasing the protection of the marine environment in Brazil is critical, not only to achieve government commitments but also to ensure marine resources are sustained through time. Effective conservation will only be attained by emphasizing relevant ecological criteria and explicit objectives to select additional MPAs. Future research is needed to identify better surrogates for marine biodiversity, more appropriate objectives for representation and persistence, and processes threatening marine biodiversity and ecosystem services. Local ecological knowledge of fishermen is a valuable asset for management plans; such knowledge provides both a detailed historical perspective of fisheries but also encourages stakeholder participation in planning, imperative for the success of implementation. Given limited knowledge of the Brazilian marine ecoregions, a participatory and adaptive approach is likely to lead to the best outcomes for conservation and sustainable use.

Chapter 3. Integrating connectivity and climate change into marine conservation planning[2]

Abstract

Most applications of systematic conservation planning have not effectively incorporated biological processes or dynamic threats. I investigated the extent to which connectivity and climate change have been considered in an ecologically meaningful way in marine conservation planning, as an attempt to help formulate conservation objectives for population persistence, over and above representation. This review of the literature identified 115 marine planning studies that addressed connectivity and 47 that addressed the effects of climate change. Of the statements identified that related to goals and objectives, few were quantitative and justified by ecological evidence for either connectivity (13%) or climate change (8.9%). Most studies addressing connectivity focused on spatial design (e.g. size and spacing) of MPAs or clustering of planning units. Climate change recommendations were primarily based on features related to MPA placement (e.g. preferences for areas relatively resilient and resistant to climate-change disturbances). Quantitative methods to identify spatial or temporal dynamics of features related to connectivity and/or climate change (e.g. functionally well-connected or thermal refugia areas) were rare, and these accounted for the majority of ecologically justified statements. Given these shortcomings in the literature, I outline a framework for setting marine conservation planning objectives that describes six key approaches to more

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[2] This chapter was published in Biological Conservation as "Magris R.A., Pressey R.L., Weeks R., Ban N.C., 2014. Integrating connectivity and climate change into marine conservation planning. *Biological Conservation* 170: 207-221, doi:10.1016/j.biocon.2013.12.032".

effectively integrate connectivity and climate change into conservation plans, aligning opportunities and minimizing trade-offs between both issues.

3.1 Introduction

Despite a rapid increase in applications of systematic conservation planning (hereafter ―conservation planning”) over the last two decades (Bottrill and Pressey 2012), challenges persist. One challenge is the dependence of successful planning on explicit goals, preferably translated into quantitative, operational objectives (Game et al. 2013; Leslie 2005; Pressey and Bottrill 2009). Conservation planning also needs to move beyond merely representing biodiversity features to ensuring the persistence and long-term viability of species assemblages (Sarkar et al. 2006), but this aspect of spatial prioritization is not yet well developed (Pressey et al. 2007). Planning for persistence, over and above representation, is inherently more complex and demanding of information. For instance, setting objectives for ecological processes can be problematic inasmuch as protection of natural processes must be based on their spatial surrogates rather than the processes themselves (Rouget et al. 2003), and requires understanding of associated spatial and temporal dynamics (Ban et al. 2012). Accordingly, relatively few studies have developed explicit objectives for persistence (but see Airamé et al. (2003), Fernandes et al. (2005), Green et al. (2009)). Thus, there is an urgent need to advance objective setting in marine conservation to guide conservation efforts, making explicit objectives more defensible and facilitating their refinement over time.

Connectivity - the movement of organisms encompassing dispersal of propagules and movement of adults - is a key mechanism underlying the persistence of populations, and hence is importance for MPA design in any region. The success of MPA networks and complementary management strategies is contingent upon the maintenance of ecological connectivity processes because larval connectivity between MPAs ensures the persistence of populations within their boundaries (Berumen et al. 2012), and larval export from MPAs to fished reefs can make a significant contribution to the replenishment of populations (Bode et al. 2012; Harrison et al. 2012). In general, areas that are periodically disturbed require functional connectivity to other areas for immigration of temporarily extirpated species (Birrell et al. 2008; Hughes et al. 2003; Salm et al. 2006) conferring ecosystems with resilience (Cowen 2007; Foley et al. 2010; Mumby and Hastings 2008). Although an understanding of connectivity is clearly crucial to effective conservation outcomes, it has been poorly incorporated into existing design protocols for MPA networks (Almany et al. 2009). In the face of major declines in fishery stocks, increasing human disturbances of marine ecosystems, and calls for ecosystem-based management, it is fundamental to maintain larval or adult exchange and recruitment of populations over demographically relevant time scales.

Climate change is of major interest for conservation because it acts simultaneously as a driver of biodiversity processes and a dynamic threat (Pressey et al. 2007), adding additional challenges to spatial planning. For example, catastrophic events related to warm anomalies in sea surface temperature can potentially negate the contribution made by MPAs to protecting a region‘s biodiversity (Game et al. 2008b). Projected future climate change will undoubtedly result in even more dramatic shifts in the distributions of species and composition of many marine ecosystems, both directly and indirectly (Lawler 2009). Protective management of large, functioning ecosystems cannot directly address such external influences on marine environments. Climate change has typically been addressed in marine planning through generic strategies or design principles with the aim of minimizing threats to ecosystems, including requiring higher representation and replication of features, and spacing protected areas to spread risk and represent differences in composition or genetics (Fernandes et al. 2005; Lawler 2009; McLeod et al. 2009; Salm et al. 2006). On the whole, however, few approaches to MPA planning have been based on knowledge of the directional or stochastic changes resulting from climate change and their effects on species and ecosystems. This limitation underlines the importance of new approaches to designing MPA networks that will help clarify management requirements for avoiding or mitigating climate-change disturbances or promoting recovery after disturbance.

Connectivity and climate change also interact. Climate-related disturbances not only disrupt larval dispersal pathways by reducing larval export from affected areas and changing hydrodynamics, but might also cause a shift in spawning phenology (earlier spawning of adults), larval transport (shorter pelagic larval durations), larval mortality (reduced exposure to lethal temperatures and shorter larval life), and behavior (increased larval swimming speed) (Cowen and Sponaugle 2009; Lett et al. 2010; O'Connor et al. 2007). The spatial scales of population connectivity might be reduced in the future due to these diverse effects on habitat fragmentation (Munday et al. 2009a). Simultaneously, connectivity can influence post-disturbance recovery and the ability of organisms to adapt to rapid climate change (Munday et al. 2008). Altered species distributions might also limit or expand the connectivity of sites in the future. Conservation planners should thus consider all possible interactions between connectivity and climate change that might act on species occurrences and abundances and influence the future efficacy of MPAs.

Despite recent literature emphasizing the need to incorporate connectivity (Almany et al. 2009; Foley et al. 2010; Fox et al. 2011; Pressey et al. 2007; Roberts et al. 2003) and climate change effects (Game et al. 2008b; Heller and Zavaleta 2009; McLeod et al. 2009; West and Salm 2003) into the design of MPA networks, little work has been done to critically examine their integration into conservation planning. Here I review approaches to incorporating connectivity and climate change into marine conservation planning to evaluate the extent to which ecologically informed strategies have been recommended or applied. I also explore what approaches have been recommended or applied to combine connectivity and climate change considerations, revealing integrative approaches and potential trade-offs. Additionally, I identify the main shortcomings of goals and objectives related to connectivity and climate change in marine conservation planning and suggest how these might be overcome in future applications.

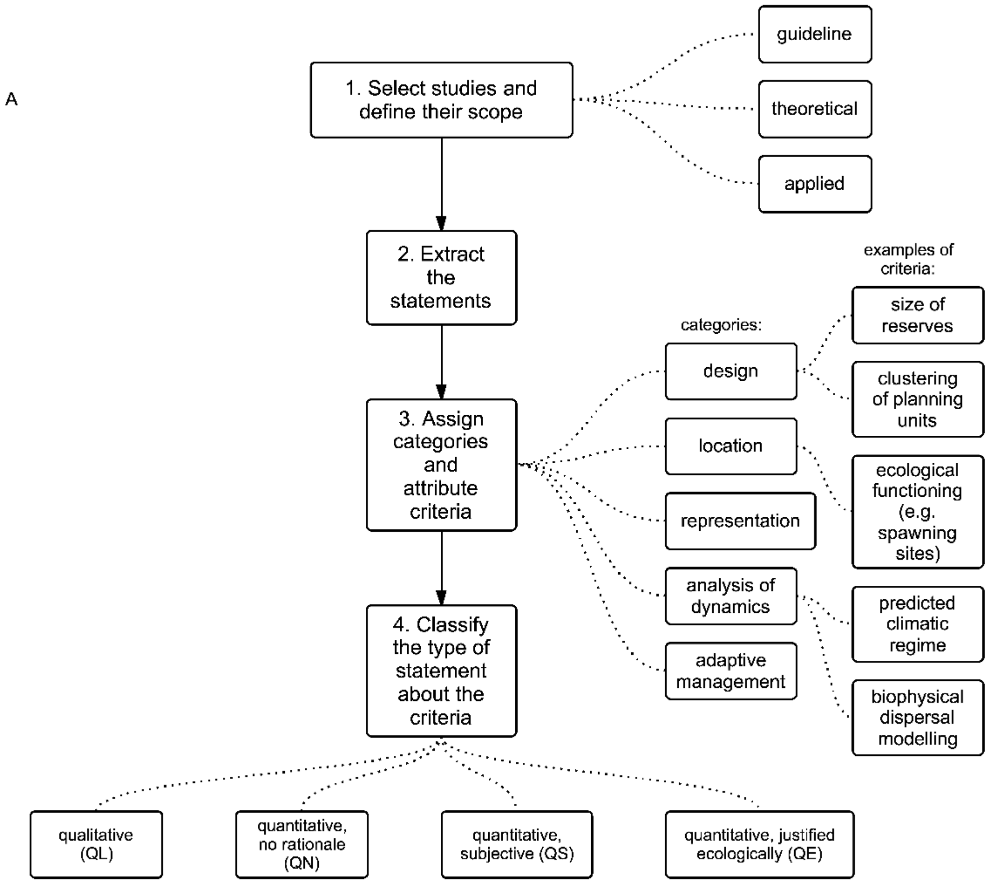
The review adds to the body of knowledge on marine planning for dynamic processes in having four key characteristics: (i) comprehensive - previous efforts have focused on particular aspects of protected area configuration such as size and spacing; (ii) synthetic - studies to date are scattered in published studies and grey literature (e.g. reports by nongovernmental agencies), so their findings are not readily available and not collated to identify patterns, trends and gaps; (iii) addressing tradeoffs between sets of objectives - tradeoffs between objectives for connectivity and climate change and opportunities for aligning them have not been adequately addressed in previous work; and (iv) marine focused - given the pronounced differences in dispersal patterns for marine versus terrestrial species and the high sensitivity of marine ecosystems to large-scale environmental change, exploring marine-based approaches is of particular relevance. More specifically, given that explicit conservation objectives are critical in shaping the subsequent stages in the conservation planning process, and that this phase is subject to frequent mistakes made by planners (Game et al. 2013; Pressey and Bottrill 2008; Pressey and Bottrill 2009), a review of marine conservation planning in relation to connectivity and climate change increases the accessibility of evidence to support more effective frameworks for decision making.

3.2 Methods

3.2.1 Database of conservation planning studies

I searched on the ISI Web of Knowledge (www.isiknowledge.com) and Google to identify peer-reviewed papers published in ecological journals, book chapters, and grey literature reports, from any year. The literature search used the terms ‗connectivity', ‗climate change', 'global warming‘, _marine conservation‘, _marine spatial prioritization‘, _marine conservation prioritization‘, _marine reserve selection‘, _marine conservation planning‘, _marine protected area‘, _marine reserve‘ and _decision support tool‘. Further studies were identified from references cited in these documents. The information for the analyses was extracted and organised in a database.

I initially scanned studies and selected for further analysis (Fig. 3.1) only those with a primary aim of: (i) proposing and designing an MPA network; (ii) evaluating how well existing MPAs were being managed, including zoning and rezoning; (iii) assessing a region‘s biodiversity or identifying areas of biological significance across a region; (iv) proposing broad guidelines for incorporating connectivity and/or climate change into marine conservation assessments, whether by proposing theoretical frameworks or offering reviews; (v) prioritizing areas for purposes other than biodiversity conservation, such as fisheries management, or based on quantitative assessment of threats; or (vi) addressing disturbance from climate change or climate-change disturbances combined with those of other threatening processes.



B

	QL	QN	QS	QE
connectivity	"Where a reef is incorporated into no-take zones, the whole reef should be included"	"MPAs should ideally be at least 4–6 km in diameter/width although smaller ones have also been effective"	"marine protected areas are spaced 1–5 km apart, distances that are likely to promote larval connectivity"	"it was determined that the distance between adjacent reserves should not exceed 100 km. A study on the dispersal of grouper larvae in the Gulf of California indicates that average dispersal distance may be on the order of 150km. Thus, it was assumed that other commercial fishes, with similar larval life-spans to that of groupers, may have similar larval dispersal distance of ~ 100km."
climate change	"replication is needed to ensure persistence in the face of environmental stochasticity and the likely effects of climate change"	"At least three separated occurrences of each conservation feature are required"	"include at least three representative examples of each habitat type in different locations, distributed over a large area to reduce the chance all would be negatively impacted by a single environmental or anthropogenic event at the same time"	"As a proxy for the probability a reef is in a degraded state due to coral bleaching, we use the mean probability of sea surface temperature (SST) exceeding 2°C above the bleaching threshold in at least one year before 2100. The bleaching threshold is the highest temperature at which no bleaching is predicted to occur irrespective of exposure time."

Figure 3.1 (A) Flowchart depicting major steps in extracting information on studies considering connectivity and climate change in marine conservation planning. (B) Examples of qualitative and each type of quantitative statement. Keywords and search criteria were used to select 134 studies that addressed or recommended marine conservation applications of connectivity and climate change. Statements referring to both connectivity and climate change were extracted to a database. Categories and criteria for designing marine protected areas were assigned to each statement to understand the range of approaches identified. In addition, statements were classified to reflect how

the criteria were applied. Qualitative statements (QL) refer to statements of preferences. Quantitative statements (involving numerical values) were grouped into three classes: no rationale (QN), subjective (QS), or justified ecologically (QE).

Applying these filters, I identified 134 studies (see Appendix C3). Of these, 115 referenced connectivity, 47 referenced climate change, and 28 considered both connectivity and climate change. Each study was placed into one of three themes according to their scope (Fig. 3.1): ―guideline" - studies providing generic recommendations for conservation planning; ―theoretical" - studies conceived as an academic exercise or exploration with no intention to inform practical applications; and ―applied" - studies undertaken with the purpose of influencing real-world conservation planning applications by involving stakeholders, supporting government planning processes, or informing a specific policy commitment.

3.2.2 Data analysis

I characterised approaches to considering climate change or connectivity following the steps shown in Figure 3.1. Statements (declarative sentences about methods of dealing with either connectivity or climate change) from each study were extracted and recorded verbatim in the database, before being coded as below. Altogether, I extracted 318 statements related to connectivity and 190 statements for climate change. Although studies conveyed information in different ways, most statements about conservation planning for connectivity and/or climate change could be assigned to five categories (see Table 3.1 for definitions): (i) design (spatial configuration); (ii) location relative to features of interest; (iii) representation of features such as species or ecosystems; (iv) analysis of dynamics; and (vi) adaptive management. The first three categories related to placement and spatial arrangement of MPAs. The last two categories referred to techniques for identifying spatial priorities for conservation management. Statements that did not fall into these categories were omitted (these were few, and extremely vague).

Table 3.1 Definition of categories of criteria for connectivity and climate change in marine conservation planning.

Category	Definition	Examples of application
Design	Spatial configuration of protected areas, planning units, or conservation features (e.g. species, ecosystems)	Number, size, spacing, and directional alignment of protected areas Replication and adjacency of features Shape and clustering of planning units
Location	Placement relative to features that are desirable or undesirable to include in networks of marine protected areas	Spawning or aggregation sites Poor water quality habitats Refugia from warm anomalies in sea surface temperature
Representation	Sampling of each biodiversity feature of interest in a network of marine protected areas, usually based on an objective for a minimum amount or frequency of occurrence	Represent a minimum amount of each bioregion in no-take areas At least 20% of each habitat type
Analysis of dynamics	Quantitative methods to characterize the spatial and/or temporal dynamics of climate-related variables or features of conservation interest	Predicted climatic regime Interpreted historical climate variability Species‘ range shifts
Adaptive management	Explicit statements about uncertainty and/or recommending revision after evaluation	Testing new approaches in response to existing and future planning activities

To explore the full range of approaches more specifically, I attributed criteria within each category to every statement. For example, statements in the `design` category could be assigned to criteria such as `size of reserves` or `clustering of planning units`. This allowed me to more accurately identify similarities between approaches. As information from each study was recorded, the criteria were re-examined to ensure consistency of definition and interpretation in the database. I then summarised the frequency with which criteria were recommended or applied across studies.

I further classified each statement as either qualitative or quantitative (Fig. 3.1). Qualitative statements were those that addressed climate change or connectivity by applying general principles or setting goals without quantitative specification, often involving statements of preferences (see Fig. 3.1 for examples). Quantitative statements involved numerical values when interpreting a principle or estimating requirements for conservation management.

Quantitative statements were further classified (Fig. 3.1) on the basis of their stated rationale as ―no rationale”, ―subjective” or ―ecologically justified”. Those with no rationale lacked any explicit justification. Subjective quantifications were based on the opinions of experts, stakeholders, or the authors, or on previous work or models, but without explicit ecological justification. Ecologically justified quantifications drew on empirical data, ecological theories, or models employed with supporting ecological information. Where statements were substantiated by a literature citation, the basis of the information provided and the context of the original cited study(ies) were investigated to classify statements as either subjective or justified ecologically.

3.3 Results

3.3.1 Overview of studies

Studies related to connectivity outnumbered those for climate change, and most studies used more than one explicit statement to address one or both issues, regardless of their scope (i.e, guidelines, theoretical or applied studies). Statements about incorporating climate change into conservation planning were predominantly (>78%) qualitative, proposing general principles or recommendations. The few quantitative statements were split between those that were subjective or ecologically justified (12.1 and 8.9% of statements, respectively). In contrast, connectivity has been substantially addressed quantitatively (>45% of statements), although rarely with an ecological justification (13%). Overall, there appears to be little ecological information on which to base guidelines for marine conservation planning to address connectivity or, especially, climate change. Most ecologically justified statements about connectivity were based on literature reviews (>57%). Conversely, the few statements about climate change classified as ecologically justified were mostly supported by calculations and/or models (>80%).

Applied studies mostly presented qualitative statements for both connectivity (58%) and climate change (79%). Only a minority of statements were quantitative and ecologically justified (6.4% for connectivity and 3.4% for climate change). In contrast, quantitative statements that were ecologically justified received the most attention amongst theoretical studies for both connectivity (60%) and climate change (>80%). The distribution between studies in each of the three scope categories varied widely through time (Fig. 3.2A,B) with no clear trends. Quantitative, ecologically justified statements increased from about 2008 (Fig. 3.2C,D), with no apparent trends in the other types. Detailed information about the distribution of statements across their types, categories, and scope of studies is reported in the Appendix C3.

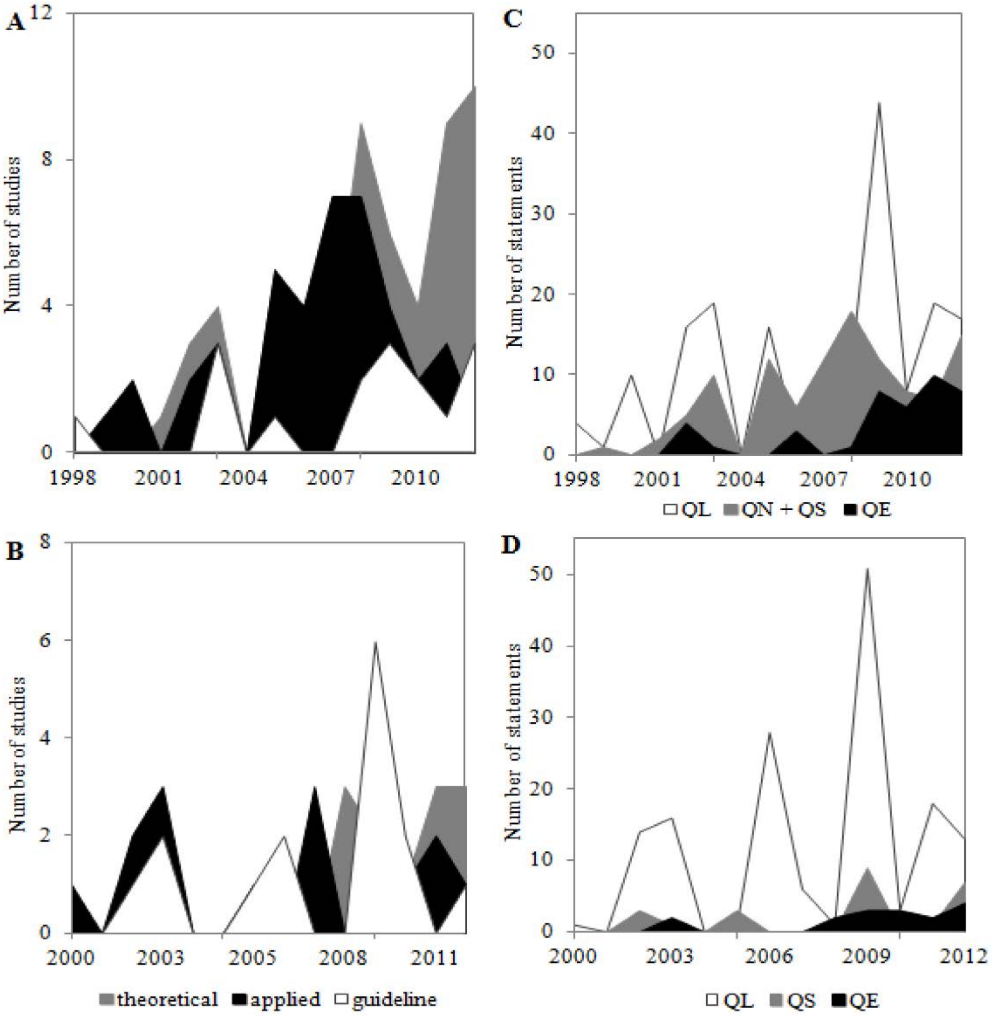


Figure 3.2 Integration of connectivity and climate change into marine conservation planning over time. Graphs indicate the numbers of studies in each scope category and numbers of statements of each type, by publication year for connectivity (A and C, respectively) and climate change (B and D, respectively). QL refers to qualitative statements; QN, quantitative with no rationale; QS, quantitative, subjective; QE, quantitative, justified ecologically. Study scopes are guideline (e.g. reviews), theoretical (e.g. novel approaches or advances), or applied (e.g. supporting government or NGO commitments).

3.3.2 Connectivity

Most case studies addressing connectivity focused on aspects of MPA network design, including (Table 3.2): clustering of planning units (72 statements), size of MPAs (26 statements), and spacing of protected areas (22 statements). Clustering of planning units was typically addressed through the boundary length modifier (BLM) in Marxan (a commonly used decision support tool for conservation planning). The use of BLM highlights the difference between quantitative, ecologically informed requirements for connectivity and, as typically applied in Marxan, a software parameter not necessarily related to actual connectivity requirements. In subjective quantitative statements, BLM values were often chosen to optimize the tradeoff between overall network cost and fragmentation of planning units (e.g. Ban et al. (2009), Giakoumi et al. (2011), Grantham et al. (2011)). Other stated reasons for BLM values included: wide distribution of MPAs (Game et al. 2011; Sala et al. 2002); a range of MPA sizes (Ban 2009); comparable size and spacing to a previous proposal (Klein et al. 2008b); and a predefined number of MPAs (Hansen et al. 2010b). In quantitative statements with no rationale, BLM values had no explicit justification (e.g. Allnutt et al. (2012), Geselbracht et al. (2008), Hinchley et al. (2007)) or BLM was used with no information on the specific value (e.g. Ban et al. (2008)).

Table 3.2 Summary of criteria used to address connectivity (115 studies) and climate change (47 studies) in marine conservation planning. Criteria are listed alphabetically within categories. Further details about how all criteria were attributed for each statement are given in the electronic database (see Appendix C3). Symbols in the interaction column indicate types of overlap between criteria for connectivity and climate change. Convergent (✓) interactions indicate that the criterion has been adopted in a complementary way for both connectivity and climate change. Undefined (?) interactions indicate that the application of the criterion could involve tradeoffs between achieving objectives for connectivity and climate change. Rows with no entries for interactions indicate that the criterion has been adopted exclusively for either connectivity or climate change.

Category	Criterion	Frequency of statements for connectivity	Frequency of statements for climate change	Interaction
Design	Adjacency of features	5	1	✓
	Buffer around features	1	2	✓
	Clustering of planning units	72		
	Directional alignment of protected areas	1		
	Juxtaposition of sources and destinations	6		
	Number of protected areas	19	7	✓
	Proximity of features	12	3	✓
	Replication of features	9	23	✓
	Shape of planning units	16		
	Shape of protected areas	6	2	✓
	Size of protected areas	26	15	?
	Spacing of protected areas	22	9	?
	Stratification of study area	5	3	✓
Location	Anthropogenic stresses	4	12	✓
	Climatic refugia	1	8	✓
	Ecological functioning	61	28	✓
	Oceanographic features	10	10	✓
	Resilient/resistant ecosystems		18	
	Topographic features	3	9	✓
Representation		13	11	✓
Analysis of dynamics	Biophysical dispersal modelling	7		
	Predicted climatic regime		9	
	Interpreted historical climate variability		13	
	Metapopulation modelling	7		
	Species' range shifts		3	
Adaptive management		12	3	✓

All types of statements considered the size of MPAs (Table 3.3). Qualitative approaches to MPA size included statements related to ‗bigger is better‘ or ‗reserves within systems should vary in size‘ (e.g. Almany et al. (2009), Fox et al. (2011), McCook et al. (2009)). Although large MPAs were typically favored, there were also instances where smaller MPAs were preferred. For example, Roberts et al. (2003) suggested that smaller MPAs spaced more widely could provide greater connectivity for long-distance dispersers. A single quantitative statement with no rationale argued that MPAs should ideally be at least 4–6 km in diameter, while acknowledging that smaller MPAs have also been effective (Fox et al. 2011). Quantitative subjective recommendations based on authors‘ opinions and expert judgments about size were provided by three studies (Fernandes et al. 2005; Fernandes et al. 2012; Lowry et al. 2009). According to Fernandes et al. (2005), for example, no-take areas should be at least 20 km long on the smallest dimension to ensure maintenance of populations. Quantitative recommendations for MPA size justified ecologically were based on previous literature. Some of these statements were precise [e.g. an optimum area of 10 km^2 (Mora et al. 2006), sizes between 10 and 100 km^2 (Weeks et al. 2010a)] while others were less so, such as MPAs ―that are several to tens of kilometers in alongshore length should be suitable to contain adult movement for much of the diversity of nearshore species” (Gaines et al. 2010).

Table 3.3 Types of statements for connectivity (unfilled squares) and climate change (filled squares) according to how each criterion has been applied in the reviewed literature. Criteria are listed alphabetically within categories. Further details about how all criteria were attributed for each statement are given in the electronic database (see Appendix C3). Examples of references are provided. QL refers to qualitative statements; QN, QS, and QE indicate quantitative statements with no rationale, defined subjectively, and justified ecologically, respectively.

Category	Criterion	QL	QN	QS	QE	Examples of studies for connectivity (c) and climate change (cc)
Design	Adjacency of features	□ ■				(c) Agostini et al. (2012); Fernandes et al. (2005) (cc) McLeod et al. (2009)
	Buffer around features	□ ■				(c) Green et al. (2009) (cc) McLeod et al. (2009); Salm et al. (2006)
	Clustering of planning units	□	□	□		(c) Ban et al. (2009); Malcolm et al. (2011); Sala et al. (2002)
	Directional alignment of protected areas	□				(c) Ferdaña (2002)
	Juxtaposition of sources and destinations	□		□	□	(c) Ardron et al. (2002); Beger et al. (2010); Mumby et al. (2011)
	Number of protected areas	□ ■				(c) Green et al. (2011); Hooker et al. (2011); Lombard et al. (2007) (cc) Green et al. (2011); Fernandes et al. (2012); Stewart et al. (2003)
	Proximity of features	□ ■			□	(c) Edwards et al. (2009); Lowry et al. (2009); Olds et al. (2012) (cc) Grimsditch and Salm (2006); McLeod et al. (2009)
	Replication of features	□ ■		□ ■		(c) Gaines et al. (2010); Green et al. (2009); McCook et al. (2009) (cc) Airamé et al. (2003); Gaines et al. (2010); Roberts et al. (2003)
	Shape of planning units	□				(c) Green et al. (2009); Geselbracht et al. (2009); Green et al. (2009); Wilson et al. (2011)
	Shape of protected areas	□ ■		□		(c) Agostini et al. (2012); Fernandes et al. (2012); Stewart et al. (2003) (cc) McLeod et al. (2009)
	Size of protected areas	□ ■	□	□ ■	□ ■	(c) Almany et al. (2009); Mora et al. (2006); Weeks et al. (2010) (cc) Allison et al. (2003); Fernandes et al. (2012); Soto (2002)
	Spacing of protected areas	□ ■		□ ■	□ ■	(c) Almany et al. (2009); Roberts et al. (2003); Weeks et al. (2010) (cc) Ardron et al. (2002); Fernandes et al. (2012); Roberts et al. (2003)
	Stratification of study area	□ ■		■	□	(c) Airamé et al. (2003); Sala et al. (2002); Smith et al. (2009) (cc) Airamé et al. (2003); Green et al. (2009); Ferdana (2002)
Location	Anthropogenic stresses	□ ■				(c) Agostini et al. (2012); Fernandes et al. (2005); McCook et al. (2009)

					(cc) Grimsditch and Salm (2006); Hansen et al. (2009); Wilson et al. (2011)
	Climatic refugia	□ ■	■		(c) McCook et al. (2009) (cc) Ban et al. (2012); Game et al. (2011); Hansen et al. (2009)
	Ecological functioning	□ ■	□	□	(c)Foley et al. (2010); Hooker et al. (2011); Lowry et al. (2009) (cc) Agostini et al. (2012); Grimsditch and Salm (2006); Hansen et al. (2009)
	Oceanographic features	□ ■			(c)Foley et al. (2010); Roberts et al. (2003); Wilson et al. (2011) (cc) Lombard et al. (2007); Salm et al. (2006); Wilson et al. (2011)
	Resilient/resistant ecosystems	■			(cc) Green et al. (2011); Hinchley et al. (2007); West and Salm (2003)
	Topographic features	□ ■			(c) Ardron et al. (2002); Hinchley et al. (2007); Wilson et al. (2011) (cc) Agostini et al. (2012); Fernandes et al. (2012); Salm et al. (2006)
Representation		□ ■	□ ■	□	(c) Airame et al. (2003); Fernandes et al. (2012); Fox et al. 2012 (cc) Green et al. (2009); McCook et al. (2009); McLeod et al. (2009)
Analysis of dynamics	Biophysical dispersal modelling			□	(c) Beger et al. (2010); Berglund et al. (2012); Treml et al. (2008)
	Predicted climatic regime	■		■	(cc) Ferdana et al. (2010); Game et al. (2008b); Salm et al. (2006)
	Interpreted historical climate variability	■	■	■	(cc) Allnutt et al. (2012); McLeod et al. (2010); Mumby et al. (2011)
	Metapopulation modelling			□	(c) Bode et al. (2012); Kininmonth et al. (2011); Watson et al. (2011)
	Species‘ range shifts	■			(cc) Lombard et al. (2007); McLeod et al. (2009); Soto (2002)
Adaptive management		□ ■			(c) Fernandes et al. (2012); McCook et al. (2009); Saarman et al. (2013) (cc) Hansen et al. (2009); McCook et al. (2009)

Spacing was addressed in similar ways to size (Table 3.3). Examples of qualitative statements are that MPAs should be close enough to reduce fragmentation and allow connectivity (Hinchley et al. 2007; Roberts et al. 2003). Quantitative subjective statements included: spacing less than 15 km (Agostini et al. 2012), no more than 20 km between MPAs (Fernandes et al. 2012), and spacing between 70 and 100 km (Fernandes et al. 2005). Ecologically informed statements with supporting references were provided by Almany et al. (2009), Fox et al. (2012), Green et al. (2009), McCook et al. (2009), Mora et al. (2006), Saarman et al. (2012), Sala et al. (2002), Weeks et al. (2010), and (Wilson et al. 2011). Although many studies focused on coral reefs, recommended spacing of MPAs to protect those habitats varied substantially from approximately 1–5 km to 100 km.

Many studies also related connectivity to the locations of specific features in the seascape (Table 3.2). At least five types of biodiversity surrogates were used in 71 studies to identify preferred or unfavoured locations linked to connectivity. Most locations were related to functional aspects of biological processes such as spawning or aggregation sites, larval source habitats, or physical or structural aspects of environments such as circulation patterns or topographic features such as marine channels. These studies mostly used qualitative statements (Table 3.3) to highlight the importance of critical sites that accumulate larvae or function as migratory pathways (e.g. Foley et al. (2010), Gaines et al. (2010), Saarman et al. (2012)). Some approaches regarding spawning sites involved subjective quantitative objectives (Geselbracht et al. 2008; Hinchley et al. 2007; Richardson et al. 2006). The identification and mapping of these functional areas was mostly done through expert workshops. Inclusion of source habitats in MPAs was always stated qualitatively, except for Sala et al. (2002) who made the sole quantitative statement, supported by ecological data, to protect source areas for recruitment and replenishment. The data for this study were mostly derived from interviews with fishermen, but the authors undertook diving surveys for validation (see Sala et al. (2003) for details).

It was apparent from this review of the 115 studies on connectivity that there were three seldom mentioned yet relevant criteria in which connectivity has been accounted for through ecologically justified statements. These criteria could accommodate a variety of specific biodiversity data that help formulate biodiversity objectives. First, proximity of features was addressed through quantitative statements intended to juxtapose areas with specific shared or complementary characteristics. For example, Edwards et al. (2010) used a cost function to select planning units representing reef and/or seagrass habitats within 10 km of significant mangrove forests. A second criterion – the juxtaposition of sources and destinations - was used to reflect the actual larval dispersal among sites, whether adjacent or distant. Beger et al. (2010b) used a modified version of Marxan‘s BLM (CSM - connectivity strength modifier) that applies a penalty if a source site in a connected pair is in the MPA network but the destination site is not. CSM has the potential to add a functional dimension to BLM‘s structural connectivity, yet still requires a subjective decision when setting the CSM value. Planners also need to weight the importance of connectivity relative to other objectives (e.g. biodiversity representation) - another subjective requirement.

Third, with a set of criteria categorised under analysis of dynamics, ten studies produced quantitative, ecologically justified statements to reflect functional aspects of connectivity and characterize their spatial and temporal dynamics (e.g. Bode et al. (2012), Treml et al. (2008), Watson et al. (2011b)). More specifically, these studies analysed dynamics through metapopulation modelling, biophysical dispersal modeling, or a combination thereof. For example, Treml et al. (2008) identified stepping-stone sites critical to local/regional connectivity based on an Eulerian advection-diffusion model of coral dispersal across the Tropical Pacific. A dynamic and spatially realistic model for several nearshore species was developed by Watson et al. (2011) using data on population dynamics and Lagrangian probability density functions. Whilst these studies were theoretical explorations that identified areas of biological significance without specifically targeting areas for conservation management, their insights into connectivity indicate strong contributions to understanding requirements for persistence.

Integration between analysis of connectivity and optimal design of network was promoted by a novel method proposed in Jacobi and Jonsson (2011). Applying the criterion of prioritizing the sites that act as both donors and recipients of larvae, they identified a potential network of MPAs that maximised metapopulation size based on eigenvalue perturbation theory. Since application of conservation planning occurs in a dynamic context in which plans must be formulated with a wide variety of criteria, a remaining challenge is to combine this framework with a larger set of conservation objectives.

3.3.3 Climate change

Studies considering climate change were more equally divided between criteria concerned with design (65 statements) and location (86 statements) than was the case for connectivity. Of the design criteria, replication was the most frequently used and was typically stated qualitatively (Tables 3.2 and 3.3). Quantitative subjective statements (e.g. protect at least three examples of each conservation feature (Ardron et al. 2002; Fernandes et al. 2005; Green et al. 2009; McLeod et al. 2009; Wilson et al. 2011) were based on expert opinion, authors‘ opinions, and precedents in previous planning exercises, but there was a lack of ecological justification for replication.

MPA size was addressed in contrasting ways for climate change. On one hand, some qualitative statements clearly proposed the importance of large MPAs in the face of ongoing global warming (Keller et al. 2009; McLeod et al. 2009; Soto 2002). Conversely, other authors argued that separate, small reserves offer greater insurance against disturbance from climate change (Ardron et al. 2002; Grimsditch and Salm 2006). In a single quantitative subjective statement, Fernandes et al. (2012) recommended that MPAs should have a minimum size of 40 ha (0.4 km^2). Quantitative, ecologically justified statements advocated insurance factors for increasing the area under protection based on intensity and frequency of severe disturbances, including or analogous to warm anomalies of sea surface temperature (Airamé et al. 2003; Allison et al. 2003). For MPA spacing, at least two qualitative statements suggested that protected areas should be concentrated to reduce the between-MPA distance (McLeod et al. 2009; Soto 2002) while most qualitative statements recommended more widely separated MPAs (Almany et al. 2009; Ardron et al. 2002; Roberts et al. 2003; Salm et al. 2006). McLeod et al. (2009) made the sole ecologically justified statement on spacing, recommending a maximum distance between MPAs of 15 km, on the basis that favouring connectivity will facilitate recovery after climate-related disturbance.

MPA location for climate change was addressed in diverse ways, almost all qualitative (Table 3.3). I identified 6 classes of features that were explicitly related to placement of MPAs taking climate change effects into account. These included: important areas for ecological functioning (e.g. source habitats, stepping-stone sites, spawning and feeding areas), sites that are relatively resilient and resistant to climate-change disturbances, specific oceanographic features (e.g. fronts, areas with high turbidity), and topographic features (e.g. low-lying coastal plains and shaded areas). Preference for resistant or resilient sites was relatively common, based on the view that undisturbed areas are more desirable for conservation management (e.g. Green et al. (2009), Salm et al. (2006)). However, Côtê and Darling (2010) speculated that altered communities might be more resilient to climate-related disturbance.

Another frequent consideration for location in relation to climate change was the avoidance of areas already under stress from human activities. Many studies recommended reducing or removing non-climatic threats as a way of buffering against the additional disturbances of climate change (e.g. Grimsditch and Salm (2006), Hansen et al. (2010b), Wilson et al. (2011)). Although refugia from climate-related disturbance have been mentioned primarily in qualitative statements (e.g. Game et al. (2011), Hansen et al. (2010b), Wilson et al. (2011)), two studies (Ban et al. 2012; Levy and Ban 2013) proposed subjective quantitative objectives related to refugia within no-take zones.

Analysis of dynamics was often qualitative (23 statements), but also had the most ecologically justified quantitative statements which involved the spatial and temporal distribution of areas under minimal thermal stress. These statements related to historic and/or future climatic regimes associated with bleaching risk for coral reefs through time-series analysis and future projections of sea surface temperatures (e.g. (Allnutt et al. 2012; Game et al. 2011; Mumby et al. 2011). Four aspects of these studies emerged as important considerations for the persistence of species. First, some of the studies that integrated dynamic analyses of anomalously high sea-surface temperatures and MPA design did not explicitly mention conservation objectives to achieve persistence (e.g. Allnutt et al. (2012)). Second, authors defined temperature anomalies or assessed thermal stress predominately through spatial and temporal thresholds. A thermal stress index - degree heating weeks (DHW) - emerged as the most influential predictor of coral bleaching, combining both intensity and duration of warm anomalies and related to ecological thresholds (e.g. McLeod et al. 2010). Third, the problem of using historic climatology as a basis for predicting probabilities of future bleaching involves the untested assumption of spatial congruence between current and future stress (e.g. Allnutt et al. (2012), Mumby et al. (2011)). Lastly, although there are many pathways of disturbance caused by global warming and a variety of conditions can induce coral bleaching, few studies considered sea level rise, irradiance, and ocean acidification (but see Ferdaña et al. (2010), Halpern et al. (2009), (Runting et al. 2013)) or investigated other variables related to thermal stress (but see Maina et al. (2008)).

3.3.4 Opportunities and trade-offs

I sought to identify whether approaches to incorporating connectivity and climate change in conservation planning were complementary, or required trade-offs between these two sets of objectives. I found that most criteria can be applied consistently to design MPA systems for both connectivity and climate change. For example, features targeted to protect against climatic disturbances (e.g. source habitats, spawning sites, upwelling areas, and oceanic fronts) were also cited as promoting connectivity amongst populations. In addition, adaptive management (whereby management strategies are progressively changed or adjusted in response to new information) is relevant to evaluating errors and uncertainties and improving objectives for both sets of considerations. Mumby et al. (2011) provided the sole study that explicitly addressed the interaction between connectivity and climate change objectives. By examining spatial patterns of thermal stress and predictions of larval connectivity, they evaluated whether adequate larval dispersal occurred among populations of corals in contrasting thermal regimes, which were defined according to different measures of acute and chronic stress.

Nevertheless, two design criteria can potentially create trade-offs for those seeking to address connectivity and climate change simultaneously (Table 3.2): MPA spacing and size. The studies that I reviewed made conflicting recommendations for optimal spatial configurations of MPAs. For example, while most studies recommended widely spaced MPAs to ensure against damaging disturbances from climate change, shorter distances between MPAs were recommended to promote connectivity. This implies loss of connectivity with better insurance against climate change, and vice versa. Divergent recommendations could also result from limitations inherent to meta-analyses, with problems arising from species selection, publication bias, and the collection of data across different biogeographic regions.

Recommendations for MPA size varied widely, from ‗bigger is better‘, to preferences for networks of smaller MPAs, to the bet-hedging ‗reserves within systems should vary in size‘. Based on this review, the required minimum MPA size to achieve climate change objectives (n=2: 0.4; 0.8 km^2) appears much smaller than that recommended to fully achieve connectivity objectives (n=11, mean=60 km^2, median=17 km^2). Consequently, MPA networks designed to achieve climate change objectives might not also attain connectivity objectives.

3.4 Discussion

3.4.1 Qualitative vs. quantitative objectives

The review demonstrates that, although connectivity and climate change have frequently been considered in marine conservation planning, these considerations have typically been incorporated through qualitative statements that are not translated into measurable objectives; furthermore, where quantitative objectives have been stated, these have rarely been justified ecologically. Of all the statements related to connectivity and climate change, only 13% and 8.9%, respectively, were quantitative and ecologically justified. Further, less than 25% and 15% of the few statements based on ecological evidence were derived from applied studies incorporating connectivity and climate change, respectively. Nevertheless, theoretical studies that use ecologically informed statements to formulate conservation objectives for connectivity and climate change are emerging, which could indicate a growing awareness of the importance of interpreting both processes in marine planning.

Quantitative objectives in conservation planning provide a clear purpose for conservation decisions, impart accountability and defensibility, help to translate spatially explicit data into decisions, interpret and operationalize broad conservation goals so that the resulting conservation priorities can be scrutinised and, if necessary, contested by interested parties (Game et al. 2013; Leslie 2005; Pressey and Cowling 2001; Pressey et al. 2003; Tear et al. 2005). When based on ecological evidence, they also produce the most scientifically robust conservation plans, enabling assessment of achievements with respect to ecologically meaningful goals, and promote scrutiny for refinement when more information becomes available (Pressey et al. 2013). Sutherland et al. (2004) also contend that a shift towards evidence-based conservation is likely to result in enhanced funding, through an improved ability to demonstrate effectiveness to donors and policy-makers. Although formulation of objectives supported by ecological evidence can require analytical methods surrounded by assumptions and caveats (e.g. see Mumby et al. (2011)), optimization for conservation has some history of dealing with uncertainty (Pressey et al. 2007), which can be reduced by deliberately including learning in an adaptive planning process (Grantham et al. 2009). Progressively tailoring models to the level of knowledge supported by primary biological data and formulating conservation objectives supported by ecological evidence help highlight knowledge gaps, thereby motivating critical thinking on conservation requirements.

3.4.2 A framework for setting objectives for processes related to connectivity and climate change

Although a substantial set of theoretical and operational conservation planning guidelines have been developed to direct practitioners (e.g. Álvarez-Romero et al. (2011), Groves et al. (2002), Margules and Pressey (2000), Knight et al. (2006), Lehtomäki and Moilanen (2013)), this review indicates that there remains a critical need to better understand approaches to setting objectives for connectivity and climate change, enabling decision makers to proactively design and deliver better strategies. I present a generic framework with this intent, encompassing a broad spectrum of possible approaches, which require varying amounts of ecological information, offer varying levels of ecological relevance (Fig. 3.3), and have different relative advantages and drawbacks (Fig. 3.4). Although this framework will need to be adapted to particular contexts, it provides a starting point for planning for persistence in which the effectiveness of objectives in promoting underlying goals can be reviewed adaptively as new techniques, datasets, and knowledge are acquired and as experience with conservation planning grows. This framework is also relevant to planning for other ecological processes that support the persistence of biodiversity (e.g. local extinctions and recolonizations, migration, patch dynamics) and ensure against dynamic threats and catastrophes other than those related to climate change (e.g. urbanization, oil spill, land-based runoff) (see Pressey et al. (2007)).

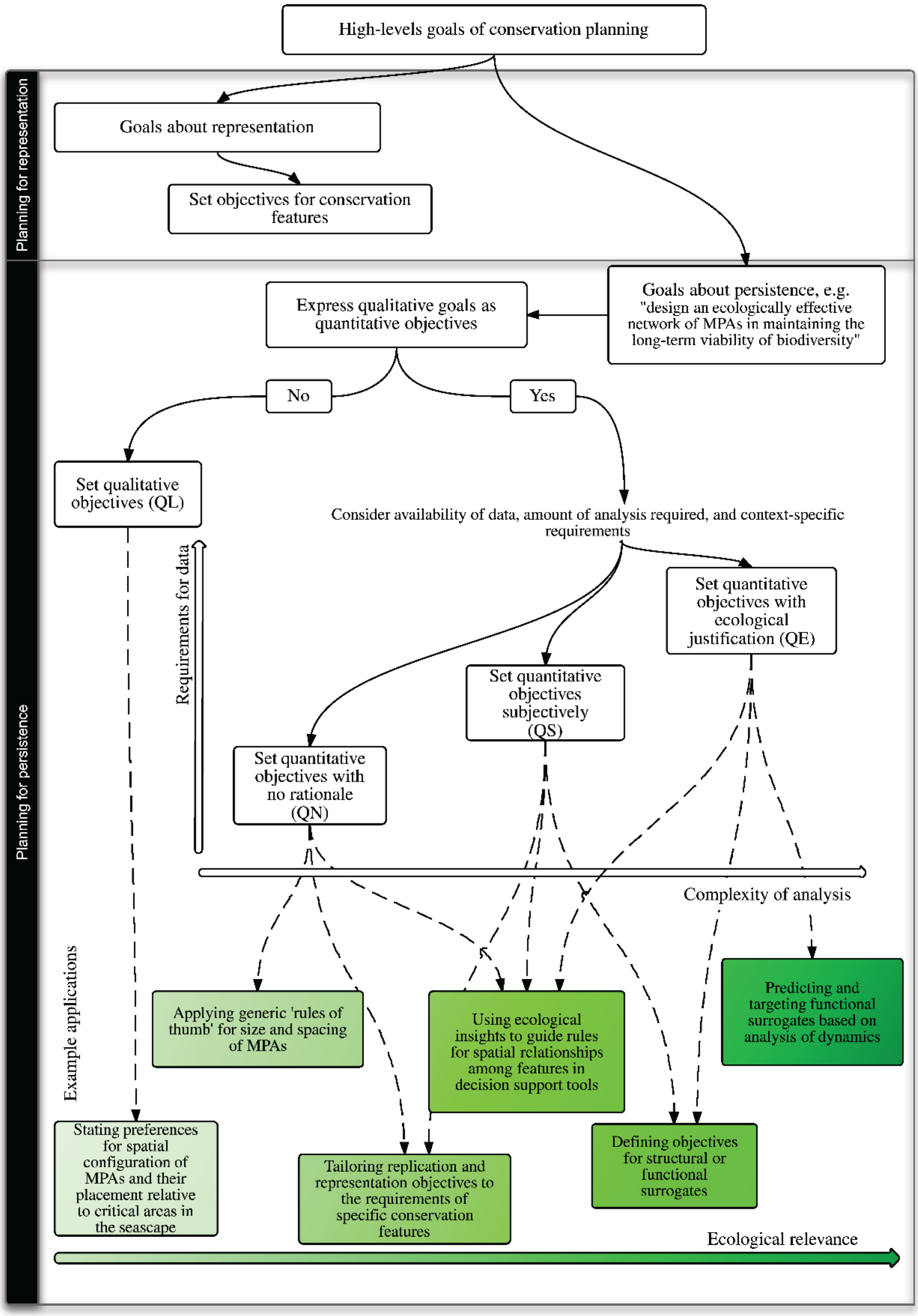


Figure 3.3 A framework for integrating connectivity and climate change into marine conservation planning through conservation objectives. The framework is based on a hierarchical relationship between qualitative and all types of quantitative statements for conservation planning addressing representation (upper portion of the diagram) and persistence (lower portion of the diagram).

Arrows represent steps toward setting qualitative and quantitative objectives. On the basis of reviewed literature, I provide examples of six approaches along a gradient of ecological relevance.

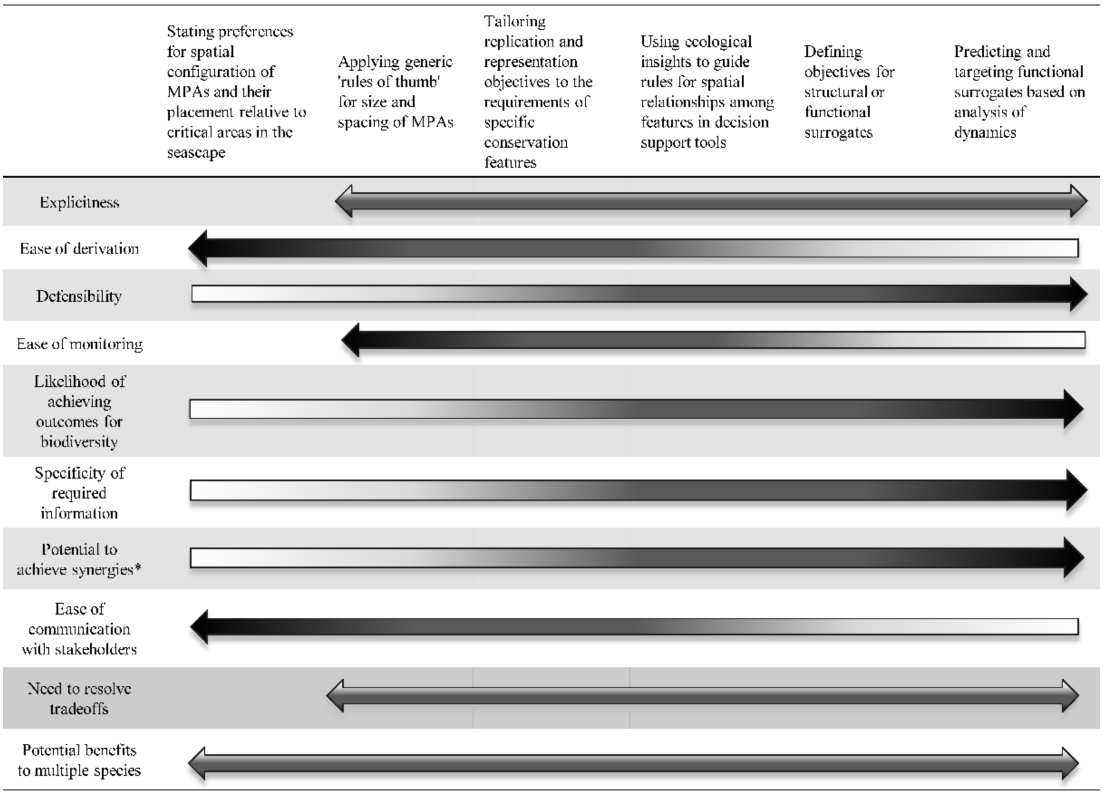


*Figure 3.4 Conceptual diagram detailing some advantages and drawbacks when applying each of the six approaches (from Fig. 3.3) to setting persistence-related objectives to plan for connectivity and climate change. Arrows combined with intensity of shading indicate the direction of change along the gradient. Bidirectional arrows with uniform shading (Explicitness, Need to resolve tradeoffs, and Potential benefits to multiple species) indicate no consistent change across the six approaches. Some considerations are not relevant to qualitative objectives. * Potential to achieve synergies refers to the possibility of achieving multiple objectives when planning for connectivity and/or climate change. This could involve achieving both types of objectives simultaneously. Alternatively, for example, planning for disturbances related to climate change could also contribute to objectives regarding other kinds of disturbances. As planning becomes more ecologically informed towards the right side of the diagram, the potential for synergies is suggested to increase.*

Conservation planning is driven by strategic goals, so initial qualitative statements (Pressey and Bottrill 2009) should be used to shape and conceptualize more specific conservation objectives (Fig. 3.3). Defining goals related to persistence is a critical first step in moving from planning for representation to explicitly considering persistence. When understanding of ecological processes is too poor to support specific quantitative objectives for persistence, planners have resorted to qualitative objectives expressed as preferences (Fig. 3.3). Where feasible, quantitative objectives based on progressively more reliable ecological data are of course preferable. In this case, planners would usually choose approaches further to the right in Fig. 3.3, although the actual order of preference might vary with context, considering factors such as availability of areas for conservation, implementation capacity, tradeoffs with fisheries or other socio-economic objectives, and spatial scale. For example, spatial mismatches between the extent and delineation of the planning region and the resolution of data or the phenomena of interest might complicate and diminish the utility of the sixth approach (targeting surrogates based on analysis of dynamics). In this situation, planners might be focused on protecting habitats at resolutions of a few km^2 while the most severe sea-surface-temperature anomalies are typically > 500 km^2 in extent (Selig et al. 2010). Also, strategic decisions about conservation actions would not be appropriate if their scale is on the order of 10s of meters or few kilometers and larval connectivity estimates are derived from regional hydrodynamic models (Treml and Halpin 2012).

The following six sections refer to the approaches listed from left to right at the bottom of Fig. 3.3.

1. Stating preferences for spatial configuration of MPAs and their placement relative to critical areas in the seascape. In the first approach, I group all qualitative criteria that fall under aspects of spatial arrangement of MPAs or preferences for areas to be managed for conservation (e.g. aggregations of key fisheries species or areas that could be naturally more resistant or resilient to coral bleaching). Collectively, although qualitative criteria have some utility in their own right when subsequent approaches are not possible, there are major concerns about the benefits that might accrue from using qualitative criteria alone (see section 4.4.1). They provide a poor basis for assessing progress in the development of MPA systems and fail to explicitly address uncertainties in conservation planning (Nicholson and Possingham 2006; Noss et al. 2012; Pressey and Cowling 2001; Sanderson 2006).

2. **Applying generic 'rules of thumb' for size and spacing of MPAs.** Generic rules of thumb offer simple, quantifiable solutions for very complex conservation concerns as a way of making decisions manageable. Determining optimum MPA size and spacing is complex due to the interactions and uncertainties around the scales of management actions and movements of organisms (Halpern and Warner 2003; Hastings and Botsford 2003; Moffitt et al. 2011b; Shanks et al. 2003). Many studies derived their statements from a single study (Shanks et al. 2003), which highlighted some marked taxonomic, geographical, and methodological biases. Using findings of one or a few studies in this way ignores the likely need to alter the source recommendations according to specific characteristics of diverse study regions. Also, meeting size and spacing guidelines has not been proved to guarantee persistence for all species that managers might wish to protect (Moffitt et al. 2011). Furthermore, this review indicates that aiming for a range of MPA sizes and spacing might be more effective in achieving multiple objectives (e.g. connectivity, climate change) than using single, specific thresholds such as specifying a maximum distance between MPAs at which populations might no longer be connected. Such thresholds are often recommended for ease of application, but have also been criticised for their inability to address the requirements of multiple species and ecosystems.

Potential tradeoffs between objectives for climate change and connectivity (section 3.3.4) arise when design criteria focus only on MPA size and spacing. Recommendations from the literature indicate that larger and more closely spaced reserves are required to achieve connectivity objectives at the expense of climate change objectives. The lack of recognition of such trade-offs can lead to unrealistic expectations and outcomes that fail to balance the two sets of considerations. For all the reasons discussed here, it is preferable for conservation planners to adopt a more skeptical view when applying rules of thumb by considering other approaches (to the right in Fig. 3.3), or adapting generic rules derived from studies of other regions to account for, as far as possible, population dynamics and other characteristics of specific study regions.

3. Tailoring replication and representation objectives to the requirements of specific conservation features. Quantitative approaches to considering climate change in marine conservation planning have largely focused on requiring replication of features within a network as insurance against disturbance events. Typically, rules of thumb for MPA network design (e.g. McLeod et al. (2009)), including those for replication, are uniform prescriptions applied to all biodiversity features, which potentially undermines their effectiveness and defensibility. More effective conservation outcomes might be achieved by refining these recommendations, for example by considering the rarity and geographic extent of each feature, intra-habitat variability in species composition or intra-specific genetic variation (Harborne 2009), the distribution and severity of expected disturbances, feature-specific vulnerability to disturbance by climate change, and aspects of dispersal of organisms of interest that determine recovery times of disturbed areas. Appropriate spacing between replicates will also depend upon the spatial characteristics of the expected disturbances, which can be informed by time-series analysis (Allison et al. 2003; Ban et al. 2012).

Similarly, objectives for representation can be fine-tuned to promote persistence. One approach is to consider insurance factors related to frequency of disturbances and estimated recovery times (Allison et al. 2003) perhaps combined with spacing protected samples of ecosystems to minimize the likelihood of all being affected by the same disturbance events (and see Thrush et al. (2005)). Another approach is to adjust objectives for features according to specific dispersal traits and available evidence concerning threats. For instance, species with short dispersal distances and/or small home ranges might decline quickly with increased localised fishing pressure and therefore require higher levels of protection across their distribution ranges.

4. Using ecological insights to guide rules for spatial relationships among features in decision support tools. Despite technical limitations, the use of decision-support tools provides insights into the planning implications of connectivity objectives and the potential gains to be made over applying rules of thumb for MPA size and spacing. This review highlighted that the most widespread approach to incorporating connectivity into marine conservation planning was by altering the value of the boundary length modifier (BLM) in Marxan (Watts et al. 2009). Whilst changing the BLM alters the importance of structural connectivity relative to other parameters (Lötter et al. 2010), it does not address functional connectivity. Therefore, if the aim is to ensure biodiversity persistence, there is an inherent limitation in BLM. This limitation is partially resolved by using the connectivity strength modifier (CSM) in place of BLM in Marxan by recognizing the asymmetry of ecological connections (Beger et al. 2010b), but neither BLM nor CSM allow species- or ecosystem-specific connectivity to be applied across multiple features.

Feature-specific connectivity can, however, be employed by Zonation - software that has rarely been used in a marine context (but see Delavenne et al. (2012), Leathwick et al. (2008)). To take account of the likely impacts of fragmentation on species protection provided by MPAs when defining the biological value of a focal cell, the boundary quality penalty (BQP) assesses consequences of connectivity loss in neighborhoods of varying size and at varying rates describing the connectivity requirements and strength of connectivity for the species (Lehtomäki and Moilanen 2013). A remaining constraint here is the inability of Zonation to include the multi-directional connectivity typical of marine ecosystems (Beger et al. 2010).

Despite these constraints on BLM, CSM and BQP, and putting aside some unsophisticated applications, tools such as Marxan and Zonation can provide valuable starting points for strengthening the ecological basis of conservation planning. Ultimately, however, decisions about the design of MPAs will require more than connectivity parameters in software. Informed decisions about connectivity will benefit from interactive and iterative use of decision-support tools by people familiar with planning regions (Pressey et al. 2013).

5. Defining objectives for structural or functional surrogates. This approach provides planners with a refined set of surrogates that might be targeted to conserve and maintain ecological processes and incorporate climate-related disturbances. The approach also lays the foundation for identifying functionally well-connected or resilient areas in the sixth approach that follows. Instead of aspiring to comprehensively assess biodiversity, objectives can be set for functional groups that sustain ecosystem processes or areas of high species richness (e.g. Hooker et al. (2011)), if these or other aspects of marine ecosystems can be established as reliable proxies for resilience to climate change or maintenance of ecological processes. This would be one way for managers to take a resilience-based approach and afford a degree of insurance against ecological uncertainty (Hughes et al. 2005). Furthermore, because some features in seascapes have been identified as proxies for both connectivity processes and resilience to climate change (e.g. source areas that ensure recruitment to damaged sites or areas that retain high diversity), these features can be prioritised when planning for multiple objectives.

Many types of surrogates have been proposed for biodiversity processes, but few have been tested. Physical seascape attributes such as marine channels, nursery habitats and upwelling areas exhibit some level of spatial or temporal predictability (Game et al. 2009), and might act as surrogates for ecological processes important to population persistence (Pressey et al. 2007), for example as predictors of spawning aggregation sites. Nevertheless, empirical studies testing the link between these spatial surrogates and the maintenance of ecosystem processes are lacking, so it is unclear which surrogates should be prioritised in planning, particularly when socio-economic constraints might prevent all conservation objectives from being achieved. Consideration of surrogates related to the effects of climate change has sometimes entailed a focus on prioritizing resistant, resilient, or otherwise undisturbed habitats. There is some debate as to whether increased resilience to climate-change disturbances is conferred by an absence of local stress, as most studies presume (Folke et al. 2002; Heller and Zavaleta 2009; Mumby and Steneck 2008), or the opposite (Côté and Darling 2010). Furthermore, resilience is understood to be conferred not by any one attribute of areas, but through a combination of physical, biological, and human-imposed conditions acting synergistically to promote recovery after disturbance. Thus, attempts to incorporate climate change into conservation planning inevitably require assumptions about the identification of resilient sites and their management requirements (Game et al. 2008a).

6. Predicting and targeting functional surrogates based on analysis of dynamics. The ability to predict spatial and temporal patterns of functionally critical sites and evaluate their relative importance to species and communities has obvious advantages for conservation planning. Prediction of dynamic features and targeting or optimizing connectivity features such as spawning sites and stepping-stone areas might simultaneously achieve many benefits for biodiversity conservation. The range of quantitative methods identified in this approach can also contribute to predictions of habitat loss and disruption of connectivity pathways under future disturbances and increase the potential to achieve synergies (see Fig. 3.4). Although integrating prediction of dynamic conservation features with reserve selection tools is not straightforward, a small number of peer-reviewed theoretical studies have demonstrated potential ways in which this could be achieved. By doing so, it might be possible to better estimate the required percentage targets for critical sites that sustain ecological processes within networks of MPAs, while also highlighting the ecological benefits of connectivity objectives.

Typically, criteria grouped under this approach detail connectivity requirements of only a few well-known focal species, forcing practitioners to extrapolate this information when drawing conservation plans for a wider range of species. For instance, Jacobi and Jonsson (2011) offered an improved link between connectivity and metapopulation dynamics and presented an optimal design of MPAs based on a specific life-history trait. However, more realistic and ideal planning efforts need to assess how MPAs will affect a broad range of target species and assess the effects of species interactions within communities. As Baskett et al. (2007) and Economo (2011) point out in their metacommunity approaches, species interactions raise an additional complication in predicting effective reserve size, spacing, and placement: under competition, only species with dissimilar combinations of traits would coexist, revealing an inherent tradeoff between representation and persistence.

By protecting important habitats and ecosystem functions, such as thermal refugia (see Ban et al. (2012)), and ensuring that a certain amount of these areas remains protected through time, an MPA system designed around dynamic features provides the foundation for ecosystem-based mitigation and adaptation strategies. Formulating the most accurate conservation objectives requires consideration of exposure, sensitivity, and adaptive capacity to climate change (Williams et al. 2008). Although current techniques to predict climate-change disturbances have focused on exposure (Dawson et al. 2011), new perspectives are emerging for integrating sensitivity and adaptive capacity in the conceptualization of objectives to make conservation objectives more informative and conservation actions more appropriate (Donner et al. 2005; Pandolfi et al. 2011). Furthermore, more reliable conservation objectives would benefit from species-specific analyses of shifting habitat suitability and inclusion of other underlying mechanisms in response to climate change such as changes in patterns of species dispersal.

3.4.3 Future prospects

Based on the review, there are at least four important research or management issues that require consideration to strengthen the management guideline presented above. First, recommendations and stated objectives should be accompanied by clear statements about their ecological rationale and any underlying assumptions to facilitate application within different geographic and socioeconomic contexts. In addition, the utility of surrogates to estimate temporal and spatial relationships between biotic and abiotic factors and how these change over time should be carefully considered and further empirical research efforts are required here. Practitioners might also consider whether dynamic surrogates, such as sea-surface-temperate anomalies, have a certain level of predictability as a means to outweigh uncertainties around their temporal and/or spatial variation. Likewise, the role played by common ‗rules of thumb‘ in achieving real outcomes for connectivity and climate change objectives remains unknown and increasing the underpinning ecological knowledge upon which to devise appropriate management guidelines would have strong benefits for conservation. Finally, further testing is needed to more fully understand the implications of metacommunity theory for marine spatial planning, considering objectives for species with distinct combinations of life-history traits and the effects of integrating competitive interactions.

3.5 Conclusions

A clear conclusion of this literature review is that, whilst connectivity and climate change have been widely considered in marine conservation planning, this has been largely through qualitative and conceptual statements that have not been explicitly translated into quantitative objectives, or supported by ecological evidence. Yet ecologically justified, quantitative objectives are critical to achieving effective outcomes through conservation planning.

Although the consideration of connectivity and climate change in conservation planning remains largely subjective, the wide range of possible approaches provides insights as to how conservation objectives for connectivity and climate change could be set to inform more effective planning. Many criteria recommended for integrating connectivity into the design of MPAs were also cited as preventing damaging disturbances from climatic disturbances, providing opportunities to integrate objectives for both. Although there is no perfect approach for any conservation plan, the framework presented here will hopefully assist planners to move towards planning for the persistence of biodiversity features by focusing on the ecological evidence base. The suggested framework contains a non-exhaustive set of complementary approaches that could be adopted for refining marine conservation planning with respect to persistence:

1. Stating preferences for spatial configuration of MPAs and their placement relative to critical areas in the seascape;
2. Applying generic ‗rules of thumb' for size and spacing of MPAs;
3. Tailoring replication and representation objectives to the requirements of specific conservation features;
4. Using ecological insights to guide rules for spatial relationships among features in decision support tools;
5. Defining objectives for structural or functional surrogates;
6. Predicting and targeting functional surrogates based on analysis of dynamics.

Strategies for considering connectivity and climate change in marine conservation planning must move towards explicit, quantitative objectives grounded in ecological knowledge. Empirical understanding of ecological connectivity processes and factors that confer resilience to climate-change disturbances is rapidly improving, and new methods to incorporate this knowledge into existing conservation planning frameworks are emerging. I show that, even in the absence of these new insights, advances can be made through careful consideration of context-specific threats and vulnerabilities when refining replication and representation objectives.

Chapter 4. Integrating multiple species connectivity and habitat quality into conservation planning for coral reefs[3]

Abstract

Incorporating connectivity into the design of MPAs has met with conceptual, theoretical, and practical challenges, which include: (i) the need to consider connectivity for multiple species with different dispersal abilities, and (ii) the role played by variable habitat quality in determining the spatial patterns of connectivity. I propose an innovative approach, combining biophysical modelling with a routinely-used tool for marine-reserve design (Marxan), to address both challenges by using ecologically-informed connectivity parameters. I showed how functional demographic connectivity for four candidate reef-associated species with varying dispersal abilities and a suite of connectivity metrics weighted by habitat quality can be used to set conservation objectives and inform MPA placement. Overall, the strength of dispersal barriers varied across modelled species and, also across species, I found a lack of spatial concordance of reefs that were high-quality sources, self-persistent, and stepping-stones. Including spatially-heterogeneous habitat quality made a considerable difference to connectivity patterns, significantly reducing the potential reproductive output from many reefs. I also found that caution is needed in combining connectivity data from modelled species into multi-species matrices, which do not perform reliably as surrogates for all connectivity metrics of individual species. I then showed that restricting the habitat available for conservation has an

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inequitable impact on different connectivity objectives and species, with greatest impact on betweenness centrality and long-distance dispersers. I used Brazilian coral reefs as a case study but my approach is applicable to both marine and terrestrial conservation planning, and offers a holistic way to design functionally-connected reserves to tackle the complex issues relevant to planning for persistence.

4.1 Introduction

Systematic conservation planning (Margules and Pressey 2000) has been widely recognised as a coherent framework for informing decision makers about conservation problems regarding protected area design and management effectiveness. While biodiversity representation and species persistence are the key goals of conservation planning (Cabeza and Moilanen 2001), most attempts to design reserve networks have focused largely on maximizing the representation of habitat types, as a proxy for biodiversity, without considering key ecological processes, such as ecological connectivity (Halpern and Warner 2003; Sarkar et al. 2006), that contribute to persistence. This is partially because representation of features is based on static elements of biodiversity, which can be more easily mapped than dynamic ecological processes (Pressey et al. 2007). Additionally, fitting connectivity analysis into conservation planning requires many further refinements and considerations (see Moilanen (2011)). Hence, an operational framework that delivers insights for practitioners and benefits conservation practice by integrating analytical approaches is timely.

Many marine species have a bipartite life-history comprising a relatively sedentary adult phase and a pelagic larval phase that can be highly dispersive (Cowen et al. 2000; Paris and Cowen 2004; Watson et al. 2011a). Larval exchange between habitat patches (hereafter ―connectivity”) is a critical ecological process structuring marine populations and conferring ecosystems with resilience, and thus important for marine planning (Botsford et al. 2009; Cowen and Sponaugle 2009; Palumbi

2004; Roberts et al. 2003; Sale et al. 2005). Population connectivity among coral-reef patches is particularly important for several reasons. First, coral-reef seascapes are inherently patchy and fragmented, and resilience of a species to human disturbances will rely largely upon species‘ dispersal ability (Almany et al. 2009; Hughes et al. 2005; Jones et al. 2007). Second, over a protracted period, larval connectivity between patches plays a significant role in determining rates and mechanisms of recruitment on both proximate and distant reef patches (Kininmonth et al. 2011). Third, quantifying these spatial patterns of connectivity improves the understanding of the current structure of biological communities, such as identifying isolated subpopulations that might face high risks of extinction (Treml et al. 2008). Unsurprisingly, there is a growing interest in larval connectivity linked to the global proliferation of MPAs to help mitigate the current decline in coral-reef systems (Mora et al. 2006).

An expanding body of empirical evidence has demonstrated the potential benefits of incorporating connectivity into conservation management (Harrison et al. 2012; Olds et al. 2012; Planes et al. 2009). However, practical application has been hampered by conceptual, theoretical, and methodological difficulties that have resulted in poor usage of available empirical evidence to inform management decisions (Magris et al. 2014). Conceptualizing natural units that constitute populations, subpopulations, or patches is a major challenge for research on population connectivity (Kool et al. 2013). Important theoretical challenges include interpretation of connectivity in ways that will guide the selection of optimal networks of MPAs in tools routinely used for design of marine reserves, and finding ways of combining connectivity with other objectives when these tools are applied (Beger et al. 2010b; Jacobi and Jonsson 2011; White et al. 2014). Decision-makers also face methodological problems in quantifying connectivity for incorporation into reserve design (Almany et al. 2009; Jones et al. 2009).

Biophysical modelling can provide powerful insights into larval connectivity and the required designs of MPA networks (Cowen et al. 2003; Sale et al. 2005; Treml and Halpin 2012; Treml et al. 2008; White et al. 2010), increasing the reliability of expectations about conservation outcomes from management decisions. Unlike empirical methods, which provide direct estimates of actual connectivity but are data-intensive and practicable for only a handful of species across limited spatial extents (Calabrese and Fagan 2004; Cowen et al. 2006), biophysical models can benefit planning in more diverse settings. These models predict potential spatial patterns of larval dispersal for multiple species from a large number of spawning sites across multiple temporal scales and recognize asymmetrical linkage strength (Paris and Cowen 2004; Treml et al. 2008; White et al. 2010).

While biophysical modelling approaches have done much to improve our understanding of larval connectivity (Cowen et al. 2006; Treml et al. 2012), most applications to management make simplifying assumptions. For example, MPA networks are typically proposed to protect multiple species, yet most connectivity studies have focused on only one or a small number of well-studied species (Beger et al. 2010b; Cowen et al. 2006; Jacobi and Jonsson 2011). Similarly, the larval output of each site is typically modelled in relation to the quantity of habitat (larger areas of habitat having greater reproductive output), even though habitat quality is known to influence reproductive output by altering growth and densities of populations (Hodgson et al. 2011) and is likely to vary within any planning region. Data on habitat quality are essential for accurate identification of release and settlement locations, reproductive outputs, and estimates of dispersal patterns (Kool et al. 2010). Simplifying assumptions about multi-species connectivity and habitat quality are likely to influence the spatial extent and distribution of ―priority” sites in planning for connected MPAs. However, the extent of this influence is unknown.

Here, I extend previous approaches to MPA network design that consider connectivity by simultaneously integrating multiple species connectivity and local habitat quality. I address these issues with a quantitative approach (Fig. 1) that incorporates connectivity into a routinely-used MPA network design tool, Marxan (Possingham et al. 2000), with key data sets derived from biophysical modelling and remote sensing. This approach improves integration of connectivity in four ways. First, I demonstrate the formulation of objectives to consider the influence of several connectivity metrics on MPA networks. Second, instead of relying on habitat area as the sole determinant of potential reproductive output, I combine spatial models for four threatening processes to predict variation in habitat quality and incorporate this variation into the calculation of the connectivity metrics used to identify priority areas. Third, I test how well planning for connectivity of multiple species achieves connectivity for individual species. Lastly, I explore the relationship between maintaining highly-connected MPAs and the total area available for conservation.

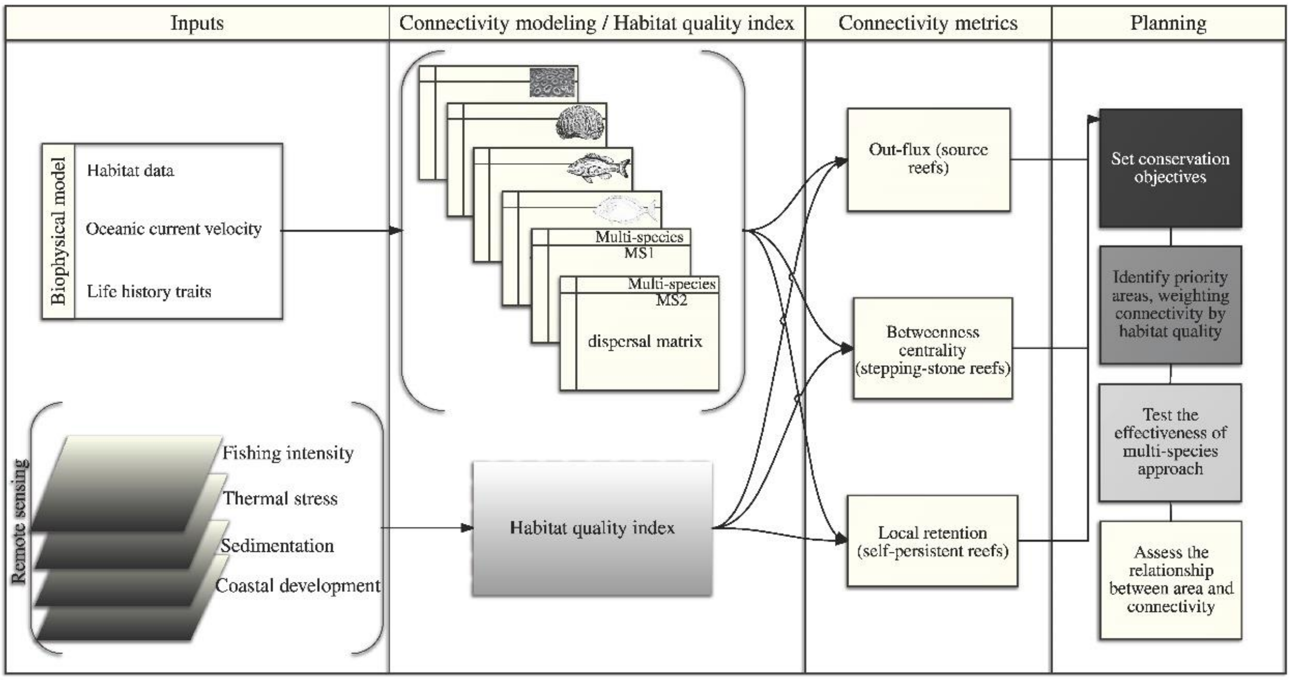

Figure 4.1 Major steps in developing my approach to integrate connectivity into conservation planning. Inputs for biophysical modelling and stressors were used to produce dispersal matrices for four candidate species and a composite index for habitat quality, respectively. Matrices for the fours species were also combined in two ways to assess multiple-species connectivity. Connectivity metrics were derived from this combined approach and used in the conservation planning software. Arrows indicate the flow of information across the major steps.

4.2 Methods

4.2.1 Brazilian reefs

I used Brazilian coral reefs as a case study. While the study region is considered a conservation priority in the southwestern Atlantic Ocean (e.g. Leão and Dominguez (2000)), coral reefs in Brazil are also faced with intensifying threats from local and global pressures (e.g. Barreira e Castro et al. (2012)). Stressors include overfishing and destructive fishing techniques (Freitas et al. 2011; Pinheiro et al. 2010), coastal development and associated runoff of terrestrial sediment (Barreira e Castro et al. 2012; Segal and Castro 2011), and disturbances related to climate change (Leão et al. 2010b; Miranda et al. 2013). Meanwhile, formal management of Brazilian marine resources is in its initial stages (Magris et al. 2013) and the ecological connectivity of reefs has not been quantified.

4.2.2 Biophysical modelling procedures

A spatially-explicit biophysical model of larval dispersal (Treml et al. 2012) was parameterised to simulate the potential connectivity among all reefs within the study region (coral reefs on the eastern and northeastern continental margins of Brazil, along 2000 km of coastline between 3° and 18°S, see Fig. 4.2A). Three components were considered in my connectivity model: (1) habitat data, (2) oceanic currents, and (3) life history traits (Fig. 4.1).

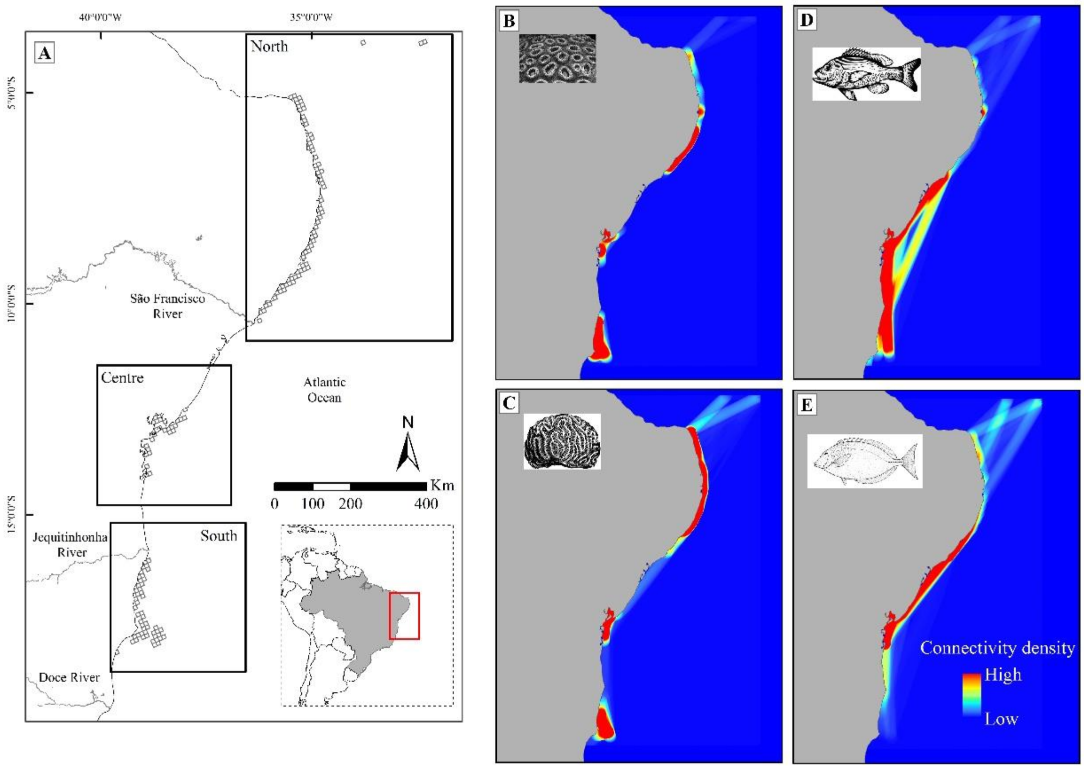

Figure 4.2 (A) The study region encompasses the north-eastern and eastern coast of Brazil (Southwestern Atlantic). 176 reef cells (10 × 10 km) were grouped into three sectors (north, centre, and south) to facilitate geographic description. (B) Connectivity density among reef cells for the brooder coral. Only demographically-strong connections are shown here. Red corresponds to the highest density of connections while dark blue refers to lowest density. Connection densities are shown using a linear stretch between the upper and lower 4th standard deviations. Connectivity density for the broadcasting coral, snapper, and surgeonfish are shown in C, D, and E, respectively.

<u>Habitat data</u>

Data on coral reef locations and extents were obtained from the Brazilian Ministry of the Environment database (Brasil 2006) which used high resolution Landsat satellite images (~30 m resolution) to map coral-reef habitats. This source provides the most current and comprehensive available information on coral reef areas in Brazil and contains more than 2,000 reef locations (approximate area of 889 km^2). Because the habitat data were at a finer resolution than the hydrodynamic data, all reef data were rescaled to the resolution of the ocean circulation model (10 x

10 km). The rescaling resulted in a grid-based model with 176 reef cells (Fig. 4.2A, upper left of Fig. 4.3), each attributed with a proportion of reef extent.

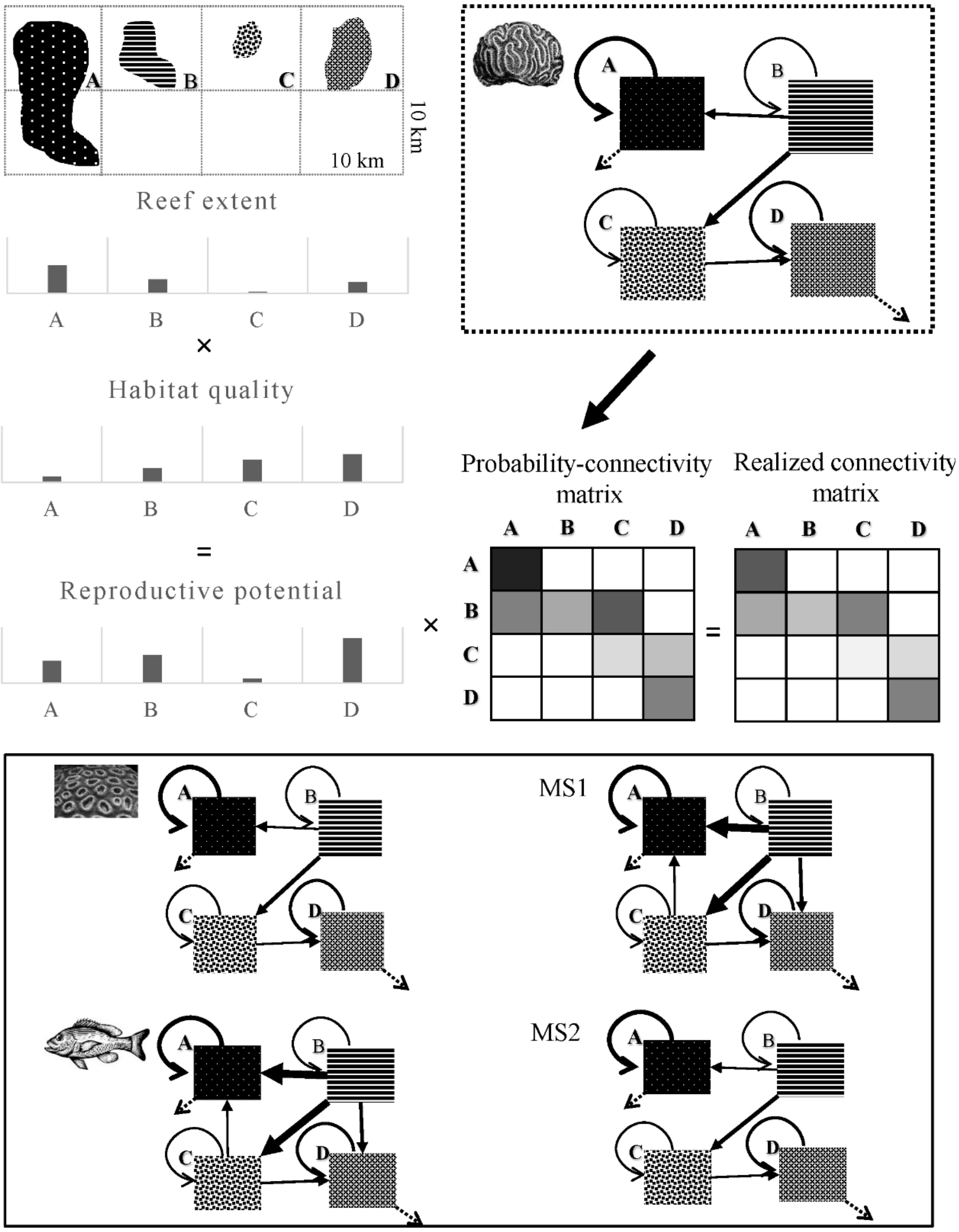

Figure 4.3 Integration of habitat quality in the connectivity models. Raw data on reef locations contained in my grid-based habitat map (10 x 10 km spatial resolution) were defined as reef cells (A-D, upper left), each attributed with proportional reef extent, habitat quality, and reproductive potential. In the upper right, connectivity networks, illustrated for the broadcast coral, were derived from the biophysical modelling, giving the probability-connectivity matrix with origins as rows and destinations as columns, filled here with shading to indicate the relative probability of dispersal between two reef cells p_{ij}. *At the centre of the figure, multiplication of the probability-connectivity*

matrix by the quality-weighted sizes of the reefs (as an estimate of reproductive output) led to the realised connectivity matrix for each species, used to calculate all connectivity metrics. I used individual dispersal matrices to formulate multi-species matrices through the MS1 and MS2 methods (in the box at the bottom of the figure). As an illustration, I use only four reef cells (A-D) and two species (brooder and snapper). The figure is further simplified by showing p_{ij} *values only in the strongest direction.*

Oceanic current velocity

Data on daily ocean current velocity from 2008 to 2012 were obtained from the Atlantic Operational Real Time Ocean Forecasting System (Atlantic RTOFS) and used to represent ocean dynamics in the dispersal model. RTOFS is an operational real-time ocean modelling system based on the eddy-resolving 1/12° global HYCOM (Hybrid Coordinate Ocean Model) (Mehra and Rivin 2010). The model uses curvilinear coordinates in the horizontal plane, and hybrid vertical coordinates in the vertical plane; it is forced by winds, rivers, tides, radiation, and precipitation fluxes over the entire domain. More information on Atlantic RTOFS is available at: *polar.ncep.noaa.gov/ofs/.*

Life-history traits

Life-history traits and reproductive strategies for four candidate taxa, representing a range of reef-associated species, were modelled based on larval-release time, spawning periodicity, larval behavior, aspects of larval competency, length of the pelagic larval stage, and larval mortality (Table 4.1). The candidate species were selected to span a large range in potential for larval dispersal. They included: two reef-builders - a brooder coral and a broadcast-spawning coral, which are essentially the two modes of larval development in scleractinian corals (Baird et al. 2009); and two reef fishes - a roving herbivorous fish (surgeonfish) and a large carnivorous fish (snapper), regarded as playing critical roles in ecological processes and having fisheries importance on coral-reef ecosystems (Bellwood et al. 2004; Graham et al. 2011). Life-history parameters were obtained from experimental or empirical observations within the study region (e.g. Pires et al. (1999), Neves and Pires (2002), Rocha et al. (2002), Neves and da Silveira (2003), Lins-de-Barros and Pires (2007), Freitas et al. (2011), Pires et al. (2011)). Although the values used for these parameters do not represent species-specific information, they reflect plausible values for keystone species with significant ecological value for coral reefs.

Table 4.1 Biological parameters used in the biophysical modelling of different life histories.

Candidate species	Brooder coral (BO)	Broadcasting coral (BR)	Snapper: large carnivorous fish (SN)	Surgeonfish: roving herbivorous fish (SU)
Larval pre-competency period (days)	3	5	14	14
Maximum pelagic larval duration (days)	15	60	30	60
Larval release time	January, February, March, 2008–2012	March, April, May, 2008–2012	February, March, September, October, 2008–2012	June, July, August, 2008–2012
Daily larval mortality	0.07	0.07	0.20	0.20
Migration-rate threshold (MRT)	10^{-3}	10^{-5}	10^{-7}	10^{-7}
Homing behavior	No	No	Yes	Yes

Connectivity modelling

The connectivity model effectively combined the data on ocean currents and biological attributes (e.g., spawning strategies, competency, mortality) to simulate dispersal among all reefs for all spawning seasons (upper right of Fig. 4.3). From each simulated spawning event, we released a cloud of virtual larvae fortnightly (for coral species) or weekly (for fish species) at reef locations in the spatial model. I measured successful larval settlement, defined as settlement that occurred when larvae reached suitable habitat, after acquiring competency, within a maximum period of time for every spawning season. The density of larvae released over each reef cell was a proportional function of the reef‘s surface area. The simulations modelled the 2-dimensional larval dispersal kernel as a ‗cloud of larvae‘ (rather than individual particles or larval tracks) directly; the cloud moved through time and space, and concentrated or dispersed according to biophysical parameters (Treml et al. 2012). The output of the biophysical model was the percentage of surviving virtual larvae dispersed between every pair of reefs. I used this information to build an asymmetric connectivity-probability matrix (centre-right of Fig. 4.3).

The connectivity strength between every pair of reef cells was defined as the probability of settling in a destination reef $\boldsymbol{j}$ from a source reef $\boldsymbol{i}$ ($\boldsymbol{p_{ij}}$); it represented potential recruitment and larval survival, and encapsulated all larval connections. To estimate demographically-explicit connections for a range of life histories, I used different migration-rate thresholds for the four candidate species to represent only those strong connections that consistently influenced local demographics over short time-scales (see Table 4.1) (Treml et al. 2012). I used this procedure because managers are concerned primarily with ecologically-significant connectivity, which is the movement of significant numbers of individuals over ecological timescales, and which will also generally ensure evolutionary connectivity (McCook et al. 2009). This movement might provide population replenishment after losses caused by diverse sources of mortality, such as bleaching, storms, or overfishing (Halpern 2003; Harrison et al. 2012; Sala et al. 2012).

I merged the connectivity data for the four modelled species to produce multi-species matrices, using two methods (bottom of Fig. 4.3). First, I used the probability of at least one connection between each pair of reef cells in any species (MS1, see equation 1, below). I termed this approach ―inclusive” because it included all sites important for the connectivity of any one species. This approach maximised the network size (i.e. total number of connections within the network). In the second approach, I considered each pair of reef cells to be connected only if they were connected for all four species (MS2, see equation 2, below). I termed this a ―strict" approach because it did not consider links between reef cells that existed for three or fewer species. By developing these multi-species matrices I was able to investigate the relative ability of the combined matrices to act as proxies for species with different connectivity requirements and yield desirable prioritization outcomes for those species. Because the multi-species approaches combined information on different species with different dispersal abilities, I generated models that I hoped would have general relevance and might aid in simplifying the use of connectivity in marine planning.

For the inclusive method, the entries in the connectivity matrix were formulated as:

$$\boldsymbol{p_{ij}}^{\boldsymbol{MS1}} = \mathbf{1} - \left[\left(\mathbf{1} - \boldsymbol{p_{ij}}^{\boldsymbol{BO}}\right) * \left(\mathbf{1} - \boldsymbol{p_{ij}}^{\boldsymbol{BR}}\right) * \left(\mathbf{1} - \boldsymbol{p_{ij}}^{\boldsymbol{SN}}\right) * \left(\mathbf{1} - \boldsymbol{p_{ij}}^{\boldsymbol{SU}}\right)\right] \qquad (4.1)$$

where $\boldsymbol{p_{ij}}^{\boldsymbol{MS1}}$ is the probability of dispersal between *cells* $\boldsymbol{i}$ and $\boldsymbol{j}$ for the multi-species matrix in the MS1 approach, $\boldsymbol{p_{ij}}^{\boldsymbol{BO}}$ is the probability of dispersal between cells $\boldsymbol{i}$ and $\boldsymbol{j}$ for the brooder coral, BR denotes the broadcasting coral, SN the snapper, and SU the surgeonfish.

For the strict method, the entries in the connectivity matrix were formulated as:

$$\boldsymbol{P_{ij}}^{\boldsymbol{MS2}} = \boldsymbol{P_{ij}}^{\boldsymbol{min}} \qquad (4.2)$$

where $\boldsymbol{P_{ij}}^{\boldsymbol{MS2}}$ is the probability of dispersal between *cells* $\boldsymbol{i}$ and $\mathbf{j}$ for the multi-species matrix in the MS2 approach, $\boldsymbol{P_{ij}}^{\boldsymbol{min}}$ is the minimum probability of dispersal between cells $\boldsymbol{i}$ and $\boldsymbol{j}$ across $\boldsymbol{P_{ij}}^{\boldsymbol{BO}}$, $\boldsymbol{P_{ij}}^{\boldsymbol{BR}}$, $\boldsymbol{P_{ij}}^{\boldsymbol{SN}}$, $\boldsymbol{P_{ij}}^{\boldsymbol{SU}}$.

The intermediate processing of the biophysical procedures therefore generated six asymmetric connectivity-probability matrices (Fig. 1), one for each species and two multiple-species matrices.

4.2.3 Remote sensing

Satellite data were used to derive proxies for habitat quality based on the following stressors: (1) fishing intensity, (2) thermal stress, (3) sedimentation, and (4) coastal development (Fig. 4.1, Table 4.2), all known to significantly disturb coral cover or fish abundance (Bellwood et al. 2004; Mouillot et al. 2013). The aim was

Table 4.2 Details of stressors that were used for developing the habitat quality model. For more information, see the Appendix C4.

Index	Data source	Method	Equation	Definitions
Fishing intensity	Google Earth Pro and government reports	Linear decay model for both artisanal and industrial fishery pressures	$\boldsymbol{F}_{\mathrm{T}} \quad \sum_{\boldsymbol{i=1}}^{\boldsymbol{426}} \boldsymbol{fd}_{\mathrm{Ti}} \quad (\boldsymbol{P}_{\mathrm{Ti}} \quad \boldsymbol{B}_{\mathrm{T}})$ $\boldsymbol{F}_{\mathrm{I}} \quad \boldsymbol{Z}_{I} \left(\sum_{\boldsymbol{i=1}}^{\boldsymbol{17}} \boldsymbol{fd}_{\mathrm{Ii}} \times (\boldsymbol{P}_{\mathrm{Ii}} \quad \boldsymbol{B}_{\mathrm{I}} \quad \boldsymbol{E}_{\mathrm{I}}) \right)$	$\boldsymbol{F}_{\mathrm{T}}$ and $\boldsymbol{F}_{\mathrm{I}}$ are the potential impact of traditional and industrial fisheries, respectively; $\boldsymbol{fd_{Ti}}$ is a distance decay factor (0−1) derived from the minimum at sea distance from the centroid of a reef cell to the ith port; $\boldsymbol{P}_{\mathrm{Ti}}$ is the number of traditional vessels in the ith port; $\boldsymbol{B}_{\mathrm{T}}$ is the difference in visual sampling efficiency of the traditional sector; $\boldsymbol{Z_I}$ - the likely fishing use of a cell based on the depth of the cell - is set equal to 1; $\boldsymbol{fd}_{\mathrm{Ii}}$, $\boldsymbol{P}_{\mathrm{Ii}}$, $\boldsymbol{B}_{\mathrm{I}}$ are the decay factor, number of vessels, and correction factor, respectively; and $\boldsymbol{E}_{\mathrm{I}}$ represents the efficiency of industrial vessels relative to traditional vessels.
Thermal stress	NOAA AVHRR sensor series	Degree Heating Weeks (DHW)	$DHW = \sum_{i=1}^{n_w} x_w$, when $x_w > 1.0$ $x_{w\,=} T_H - T_M$	x_w is the HotSpot; T_H is a weekly mean of sea surface temperature; T_M is the warmest weekly temperature in the time series; and n_w is the number of weeks = 12 weeks.
Sedimentation	MODIS Aqua	Diffuse attenuation coefficient at 490 nm (K490)	$WCI_{\mathrm{K}} \quad k490$	The value of K490 represents the rate at which light intensity at 490 nm is attenuated with depth.
Coastal development	DMSP/NOAA/NGDC nighttime satellite imagery	Light proximity index LPI	$LPI = \sum \frac{L_1 \ldots . n}{D_1 \ldots . n}$	D is the distance from the centroid of a given reef cell to the centroid of a given light pixel in the night-light imagery, and L is the intensity recorded within that given light pixel.

not to produce an accurate predictor of ecological responses to human pressures, but to develop a plausible index to test the influence of habitat quality on connectivity metrics.

Reef cells with poor quality were those closest to large human communities, heavily overfished, with the poorest water quality, and subject to high thermal stress; such reefs are typically characterised by substantial losses of coral cover, proliferation of macroalgae, and marked reductions in fish biomass (Dinsdale et al. 2008; Hughes 1994).

Stressors

An index of relative fishing intensity was derived from mapping methods originally provided by Rowlands et al. (2012) where the potential impact of traditional and industrial fisheries were estimated based on a decay factor function – fishing intensity on a particular reef cell declines linearly with distance from a fishing port or fishing lands. Identification of active vessels and fishing ports (using Google Earth Pro) was complemented with governmental reports about fishery statistics, which provides morphological characteristics of the fishing fleet and their geographic variability across the study region. In combination, they provide the most comprehensive and updated information on fishing intensity available across an extensive spatial area.

The spatial pattern of thermal stress was based on the index of acute stress Degree Heating Weeks (DHW), which is the most influential predictor of coral bleaching. By using time series data obtained from the publicly-available National Oceanic and Atmospheric Administration (NOAA) Advanced Very High Resolution Radiometer (AVHRR) satellite imagery, I collected spatial data relating to the annual maximum DHWs for each coral reef cell.

I based a water-clarity index on the diffuse attenuation coefficient at 490 nm (K490), which represents the rate at which light intensity at 490 nm is attenuated with depth. Satellite imagery was retrieved and spatially subset from MODIS Aqua. The coastal development index was calculated as originally proposed by Rowlands et al. (2012), whose index is measured by a distance from emission of night-time lights provided by the Defense Meteorological Satellite Program (DMSP) produced at the National Oceanic & Atmospheric Administration, National Geophysical Data Center (NOAA/NGDC). More details on the calculation of the proxy measures of stressors are in Appendix C4.

Habitat quality index

I combined each of the stressors presented above, to produce a composite index of the impact of cumulative threats on the release of larvae from individual cells (Fig. 4.1). Each factor individually, as well as the composite index, was normalised to the reference range of zero to one (zero indicating poorest-quality habitat and 1 representing best-quality habitat), as follows:

$$HQI = \frac{(RFI + TSI + WCI + CDI) - (RFI + TSI + WCI + CDI)_{\min}}{(RFI + TSI + WCI + CDI)_{\max} - (RFI + TSI + WCI + CDI)_{\min}} \qquad (4.3)$$

where $\boldsymbol{HQI}$ is the index of relative habitat quality, $\boldsymbol{RFI}$ is the fishing-intensity index, $\boldsymbol{TSI}$ is the thermal-stress index, $\boldsymbol{WCI}$ is the sedimentation (water-clarity) index, and $\boldsymbol{CDI}$ is the coastal-development index. The subscripts $\boldsymbol{min}$ and $\boldsymbol{max}$ of equation 3 indicate the minimum and maximum overall score, respectively, of any reef cell across the study region. The modelling approach therefore allowed ongoing threatening processes to be integrated as a function of the number of larvae exchanged between cells, taking account of both the quality and sizes of reefs.

4.2.4 Connectivity metrics

Three connectivity metrics were used to identify areas where conservation efforts could have long-term effectiveness: out-flux, betweenness centrality, and local retention (Fig. 4.1). Out-flux is related to the source-strength of a patch (a reef cell in my spatial model), and those with high out-flux have large reproductive outputs and a greater potential number of emigrants than immigrants, so are able to sustain populations of surrounding patches through their outgoing connections (Figueira 2009; Minor and Urban 2007). Betweenness centrality can help in the identification of stepping-stone patches. The metric emphasizes the ‗most used‘ dispersal pathways, and might indicate patches that control flows through the network, those that link important sources to other patches, or that would provide a mechanism of spreading risk (Minor and Urban 2007; Treml et al. 2008; Urban and Keitt 2001). Local retention is interpreted as the proportion of larvae released from a source patch that settled back to that patch (Treml et al. 2012). A patch with high local retention can contain demographic characteristics (survival and fecundity) that make it more likely to be self-persistent (Burgess et al. 2014; Figueira 2009)).

Probability matrices from all four candidate species and the two multiple-species approaches were converted to realised dispersal matrices by calculating larval flux between patches, adapting the formulae of Urban and Keitt (2001) (see centre of Fig. 4.3):

$$f_{ij} = RPO_i \times p_{ij} \qquad (4.4)$$

$$RPO_i = \frac{s_i}{s_{\text{tot}}} \times HQI_i \qquad (4.5)$$

where, f_{ij} is the expected dispersal flux from patch i to patch j, RPO_i is the reproductive potential for a given reef cell i, p_{ij} is the probability of settling on cell j from i, s_i is relativised as the proportion of total habitat area s_{tot}, and HQI_i is the habitat quality index for reef cell i (defined in the previous subsection). I then summed all fluxes for all outgoing links to determine out-flux for each particular reef cell. Betweenness centrality was measured by finding the shortest path between every pair of patches on the realised matrices, then counting the number of times those paths crossed each patch (Minor and Urban 2007). I measured local retention for each cell as the diagonal elements of realised dispersal matrices (Treml et al. 2012).

4.2.5 Planning for connectivity

I sought to optimize total connectivity benefits of a network of notional protected areas by considering all the connectivity metrics described here. I set conservation objectives for each connectivity metric to represent crucial reefs in a network of reserves that would provide the best chances of recovery after disturbance, maintain fisheries, or serve as important pathways (Fig. 4.1). I used Marxan, a tool for systematic conservation planning, to identify sets of areas (from the 176 reef cells) that achieved a specified objective for each conservation feature while minimizing a cost function (Possingham et al. 2000). Conventionally, conservation features in prioritization algorithms are individual species, habitat types, or ecosystems. In my analyses, I used the three connectivity metrics for the four candidate species and the two multi-species matrices after normalizing each of them, giving a total of 18 conservation features. For each reef cell, I also recorded the cost as equal to the reef area.

To select priority areas (Fig. 4.1), I specified the quantities at which conservation features (combinations of metrics and candidate species) should be represented in the MPA network. I found the subset of reef cells that had the top third of values for each conservation feature, and used their summed values across all reef cells to set objectives expressed as percentages of totals. For example, reef cells in the top third of values for the combination of brooder coral and out-flux had 65% of the total value across all reef cells, so this percentage became the conservation objective. Across all features, objectives varied from 45 to 67% of total values. Consequently, the approach simultaneously prioritised reefs with greater potential to support a self-sustaining subpopulation without input from other reefs (local retention), those with a potential number of emigrants greater than immigrants (out-flux), and those situated in the most frequently-used dispersal pathways (betweenness centrality).

In the first scenario, I created 100 solutions to identify the set of planning units that met the conservation objectives at least cost. These objectives were indicative, and might not be realistic, considering how little has been done to protect Brazilian marine environments (Magris et al. 2013). Therefore, I ran a second scenario with the same objectives but constrained by a maximum cost of selected reef area set at 10% of the total in the study region. I then compared the outputs of both scenarios, using both best solutions and selection frequencies, or the number of times each reef cell was selected out of 100 runs. Areas that had a selection frequency of more than 75 in my analyses were considered the highest priorities. A boundary-length modifier (BLM) was chosen following calibration for each scenario using the calibration tool in Zonae Cogito software (a user-friendly interface with Marxan).

To test the effectiveness of each multi-species approach at representing connectivity for each of the four candidate species, multiple pairwise comparisons were performed in four steps. First, I ran 12 additional scenarios in Marxan for each combination of connectivity metric ($n = 3$) and species matrix ($n = 4$) individually, and recorded the subset of reef cells selected for each of 100 repeat runs for each scenario, as well as the value of the respective connectivity metric. Second, I ran 6 other Marxan scenarios for each combination of connectivity metric (*n* = 3) and multi-species matrix *n* = (2) and recorded the subset of selected reef cells for each of 100 runs without assigning any metric value derived from multi-species matrices to them. Third, I associated reefs cells selected in the previous step to each of the connectivity metric values derived from each of the species matrices. For example, when assessing the effectiveness of MS1 as a surrogate for out-flux/brooder, reef cells selected for scenario MS1/out-flux were assigned the out-flux metric values based on the dispersal matrix for the brooder. Finally, for each connectivity metric, I examined the differences between connectivity values across 100 runs derived from reef cells selected from Marxan scenarios for each focal species and reef cells selected from Marxan scenarios for each multi-species matrix. I tested for differences with one-way ANOVA followed by Tukey‘s post-hoc test.

Finally, I assessed the relationship between each connectivity metric and area selected for conservation by variably constraining the total area (or cost) available for protection within the reserve system. This was done by dropping the cost threshold by decrements of 5% from the total cost incurred by the first scenario until the total area selected matched that with the 10%-threshold of the second scenario. Because I used the best solution outputs from Marxan for this analysis, each point of the curve represented the maximum connectivity that could be represented by protecting this amount of area.

4.2.6 Dataset and analysis caveats

Ideally, including more direct measures of reef quality (e.g., coral cover or fish biomass) within my composite index for habitat quality might have provided a more accurate integration of this information into connectivity models. However, this was not realistic because collection of standardised field data over such a large area was beyond my available resources. Instead, the habitat-quality model was based on proxies. For the same reasons, proxies for threats have been used extensively for conservation assessments and are considered as suitable alternatives to direct data on ecosystems states now or in the future (e.g. see Maina et al. (2008), Rowlands et al. (2012)). Additionally, this premise is supported by strong positive relationship between estimates of threatening processes and empirical data on habitat quality (Halpern et al. 2008). The principal concern was the potential effect of habitat quality, assessed with plausible spatial variables, on modelled connectivity and prioritization outcomes.

A significant consideration in planning is temporal explicitness of data. I was unable to address temporal dynamics associated with the stress factors and connectivity metrics. The proxies for habitat quality are likely to change over time, and the connectivity metrics will change accordingly, emphasizing the need for regular updating of such data if prioritizations for conservation are to remain current and relevant to decisions (Pressey et al. 2013).

An important assumption of the modelling was that larval output was linearly related to density of adults. To estimate the habitat quality index I also excluded potential interactions between threats and had to aggregate the variables considering different timeframes. Although the data on fishing intensity constitute to date the most spatially coherent assessment of this stressor on Brazilian reefs, a detailed mapping of fishery pressures will demand a more nuanced approach. While the spatial information I used in this modelling can reflect the impact of widespread human influences, the stressors are likely to interact differently in different parts of the study region, making predictions of ecological responses uncertain.

4.3 Results

Inter-specific differences in dispersal ability were clearly visible (Fig. 4.2B-E). By assessing demographically-relevant connections for the brooder species I was able to identify three major assemblages of reef cells (―sectors”) with connections within but not between sectors (Fig. 4.2B): (i) coastal banks off the northeastern coast – termed ―north” sector in Fig. 4.2A, (ii) a mixture of fringing reefs and banks in northern Bahia State – ―centre” sector in Fig. 4.2A, and (iii) a southern Bahia area with coastal and outer arcs of reefs in the Abrolhos region – ―south” sector in Fig. 4.2A.

Although these three sectors were still evident for the broadcast coral, its higher dispersal ability led to some connections between sectors and, in the north sector, between fringing reefs bordering oceanic islands and nearshore reefs (Fig. 4.2C). For the snapper, connectivity between the central and south sectors was particularly strong (Fig. 4.2D). The surgeonfish was also generally well-connected across the study region, and particularly in the north and central sectors (Fig. 4.2E). The three better-connected taxa have protracted pre-competency periods and drift in the plankton over long periods until they encounter suitable substrata for settlement (Table 4.1). The biological parameters for these long-distance dispersers indicated that they tended to settle furthest from their natal reefs; the brooder coral might be regarded as a short-distance disperser.

The spatial pattern of reef extent across reef cells was generally correlated with habitat quality across the study region (Fig. 4.4A and 4.4B). However, incorporating habitat quality into biophysical models reduced the potential reproductive output throughout study area (Fig. 4.4C). Across reef cells, extent weighted by habitat quality caused reductions in reproductive potential, estimated by extent only, from 0.2% to 100% (mean: 74%, median: 92%). Consequently, the proxies for habitat quality led to a large effect on connectivity quantities, ranging across reef cells from 0% to 100% for all metrics. For the source strength of reef cells, mean and median decreases were greater for the surgeonfish (94% and 99%, respectively). For local retention, the highest mean and median reductions occurred for the snapper (92% and 99%, respectively). For betweenness centrality, highest mean and median reductions were for the brooder (47% and 49%, respectively).

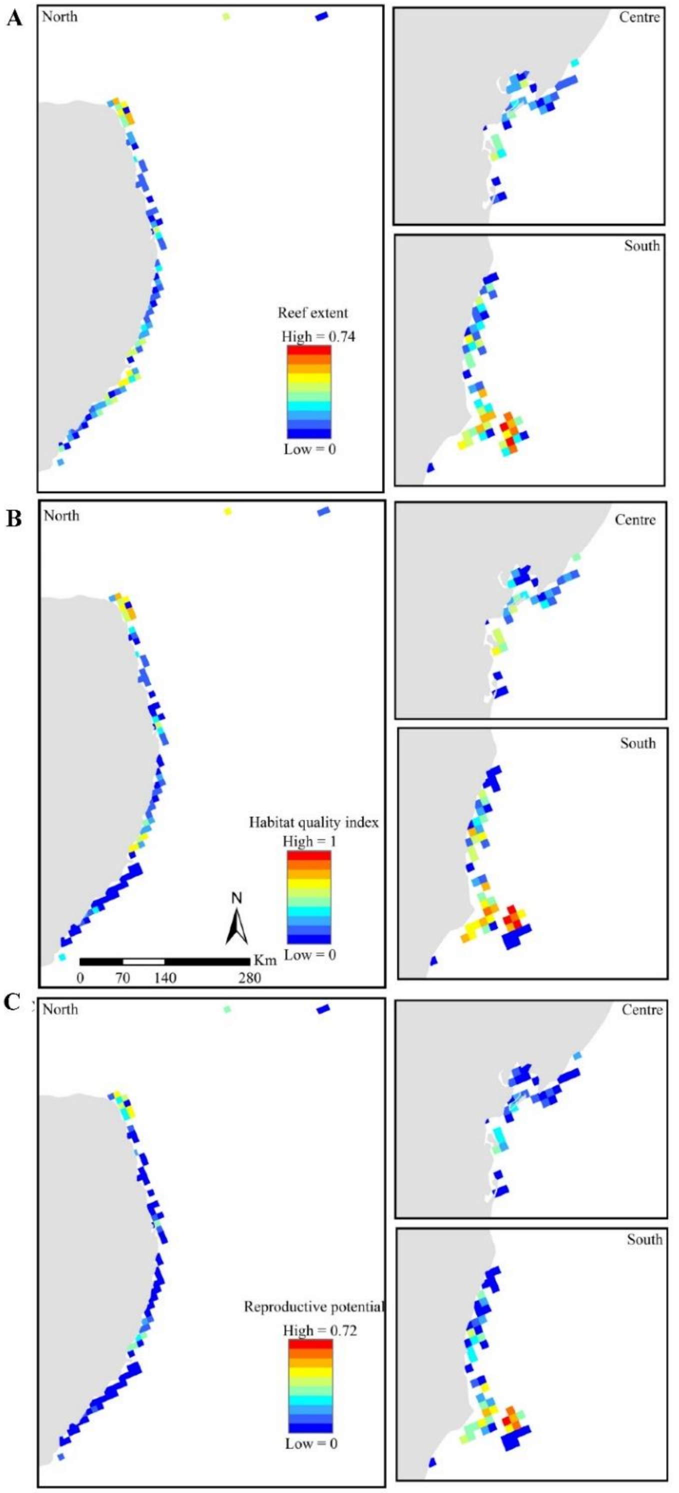

Figure 4.4 Influence of habitat quality. Values for extent of reefs (A), habitat quality index (B), and extent weighted by habitat quality (reproductive potential) (C) in reef cells. My spatial model of habitat

quality produced a spatially-heterogeneous composite index that indicated the combined exposure of reef cells to fishing pressure, thermal stress, sedimentation, and coastal development.

Comparison between connectivity metrics for each species showed that reefs important for source strength were not often also self-persistent or routes of travel by larvae across the seascape. For instance, important reefs in terms of out-flux for the brooder were only in the south sector while stepping-stone reefs were mostly in the north and centre (Fig. 4.5). Some similar spatial patterns of connectivity metrics were apparent across species (Fig. 4.5, Fig. 4.6 and Appendix C4). First, there were common spatial patterns of large values for out-flux. Many of these reef cells were in Parcel das Paredes and the Abrolhos Bank in southern Bahia. Second, similar areas had high values for betweenness centrality across coral species, including some reef cells in the north (e.g. Cape of São Roque reefs) and the centre (e.g. Itaparica reefs) and across fish species, including some reef cells in the south (e.g. Cabrália reefs). Third, there was broad spatial correspondence of self-persistent reefs across all four species, including high local retention in the north (e.g. Cape of São Roque reefs), the centre (e.g. Tinharé reefs), and the south (e.g. Sebastião Gomes and Itacolomis reefs). However, despite some level of spatial agreement of connectivity metrics across species, I found that spatial priorities changed when I progressively incremented the number of species considered (see Fig. C4.5 in the Appendix C4).

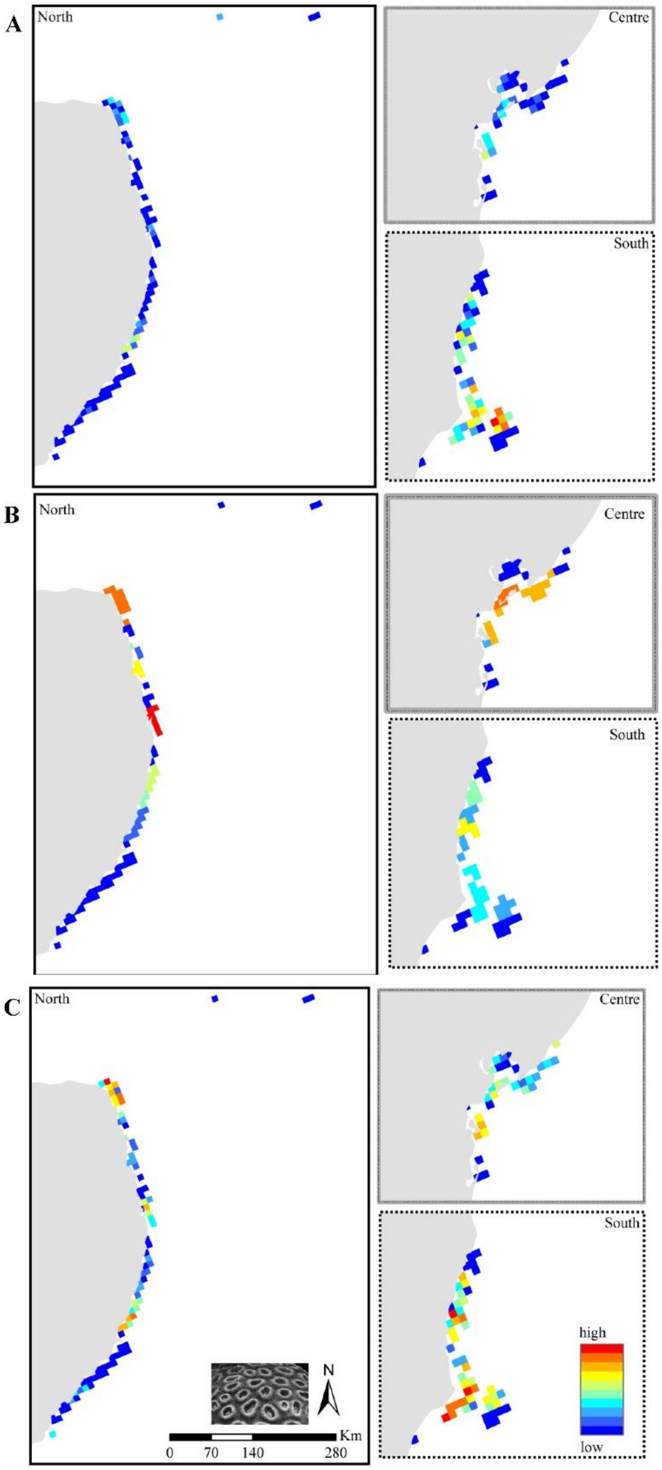

Figure 4.5 Spatial distribution of connectivity metrics for the brooder coral in Brazil: (A) out-flux, (B) betweenness centrality, and (C) local retention. See Appendix C4 (Figs. C3.3 and C3.4) for corresponding data on the broadcasting coral and the snapper.

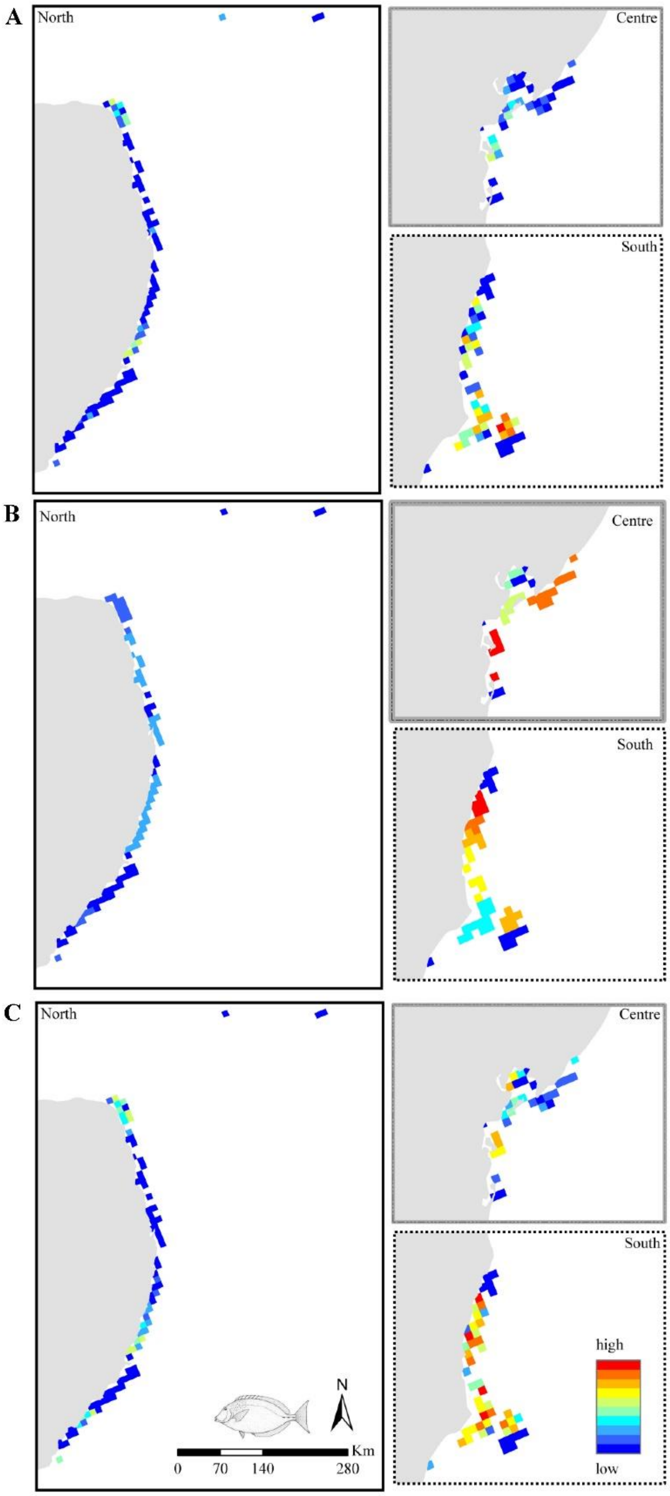

Figure 4.6 Spatial distribution of connectivity metrics for the surgeonfish in Brazil: Spatial distribution of connectivity metrics for the surgeonfish in Brazil: (A) out-flux, (B) betweenness centrality, and (C)

local retention. See See Appendix C4 (Figs. C3.3 and C3.4) for corresponding data on the broadcasting coral and the snapper.

Approximately 45% of the total reef area was required to achieve the objectives for all connectivity metrics and all species without any restriction on habitat availability (scenario 1, Fig. 4.7A). With the constraint of a 10% cost threshold (scenario 2), reef cells located in the Cape of São Roque, Cabrália, Itacolomis, Parcel de Paredes, and Parcel dos Abrolhos remained key priority areas based on selection frequencies (Fig. 7B).

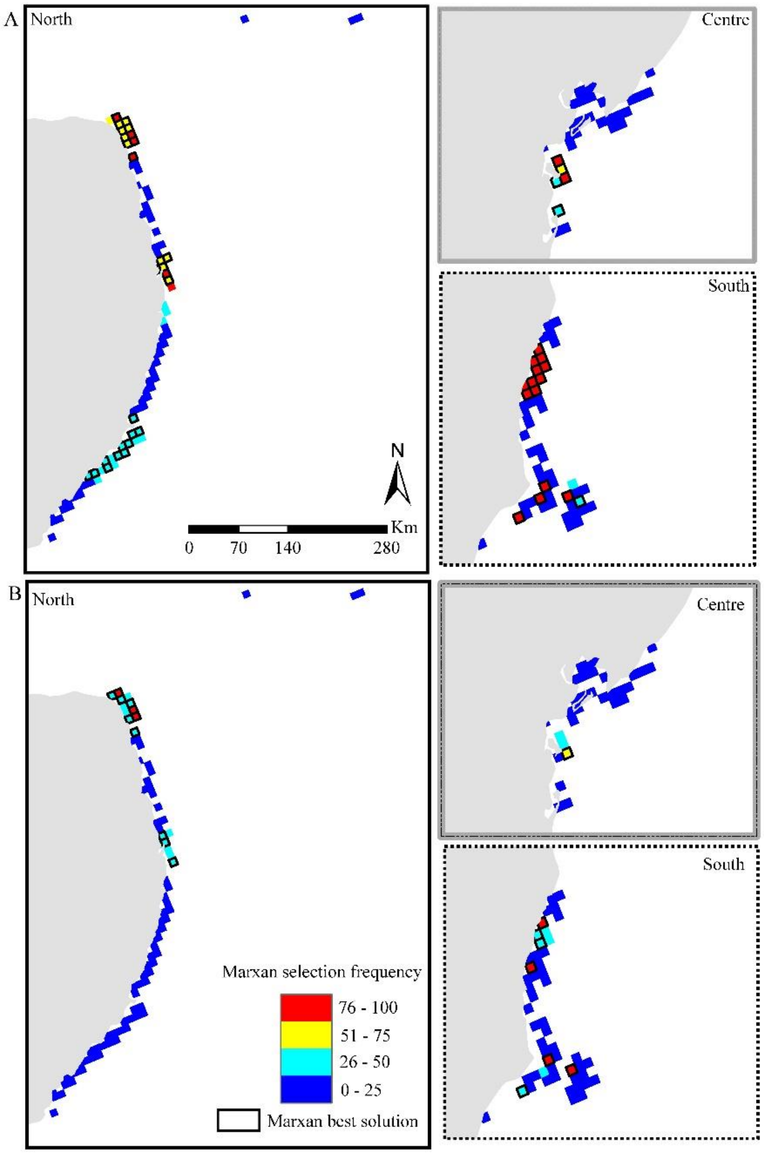

Figure 4.7 Selection frequencies and best-solution outputs from Marxan. Conservation objectives are based on top-tercile values for each conservation (connectivity) feature with no restriction in terms of coverage (A) and constrained by a maximum cost (10% of total extension of reefs, B).

About 27% and 12% of reef cells were selected in the best solutions for scenarios 1 and 2, respectively. About 11% of reef cells were included in the best solution for both scenarios. About 20% and 4% of reef cells were selected as high priorities (selection frequency > 75) in scenarios 1 and 2, respectively. About 4% of reef cells were selected as high priorities in both scenarios. The mean selection frequency of reef cells for scenario 1 (26.7) was well above that for scenario 2 (7.8). I also found that imposing the cost constraint of scenario 2 had uneven effects on connectivity across species and metrics. For example, comparisons between connectivity values for frequently selected planning units (>75) in both scenarios indicated the greatest reduction was in betweenness for snapper (nearly 60%) and the smallest reduction was in out-flux for the broadcast coral (about 8%).

The multi-species methods varied in their effectiveness as surrogates for connectivity of individual species (Table 4.3 and Appendix C4). Both multi-species methods performed reasonably well for out-flux, with no significant differences between their connectivity values and those from solutions focused on each species individually. MS1 and MS2 did less well for the other two metrics, lowering connectivity for some species (e.g. betweenness centrality for the brooder using MS2, and local retention for the surgeonfish using MS1). However, both methods scored higher than solutions for individual species in four cases (e.g. betweenness centrality for the broadcasting coral using MS1, and local retention for the snapper using MS2). Across species and connectivity metrics, MS2 outperformed MS1.

Table 4.3 Assessment of the effectiveness of multi-species matrices in achieving connectivity for individual species for each connectivity metric. Symbols in the columns MS1 (inclusive method) and MS2 (strict method) indicate the results of ANOVA and post-hoc tests for each comparison across 100 runs with P < 0.001. "☺" indicates that the multi-species approach produced significantly more connectivity than the matrix for the species; "✓" shows that no difference was found; "✗" and shading indicates that the multi-species approach produced significantly less connectivity than the matrix for the species. More details of the ANOVA are in Appendix C4.

		MS1	MS2
Out-flux	Brooder BO	✓	✓
	Broadcasting BR	✓	✓
	Snapper SN	✓	✓
	Surgeonfish SU	✓	✓
Betweenness centrality	Brooder BO	☺	✗
	Broadcasting BR	☺	✗
	Snapper SN	✗	✓
	Surgeonfish SU	☺	✓
Local retention	Brooder BO	✗	✓
	Broadcasting BR	✗	✓
	Snapper SN	✓	☺
	Surgeonfish SU	✗	✓

Restricting to 10% the total reef area available for achieving the conservation objectives markedly affected the overall connectivity value of my notional MPA network, with the greatest impacts on betweenness centrality and local retention (Fig. 4.8). At 10% of total reef area, MPAs were most likely unable to guarantee minimal requirements for the maintenance of critical stepping-stone patches for all species (only 0.05 - 1.5% of the total betweenness centrality was protected). Local retention was more linearly affected than betweenness by reductions in habitat availability, and out-flux was not greatly affected by these reductions. While the shape of the curves differed between species for betweenness centrality, there were only slight differences across species for local retention and almost no differences for out-flux. For betweenness centrality, the surgeonfish was more susceptible to restrictions on total area protected, with steep drops at the first few incremental reductions.

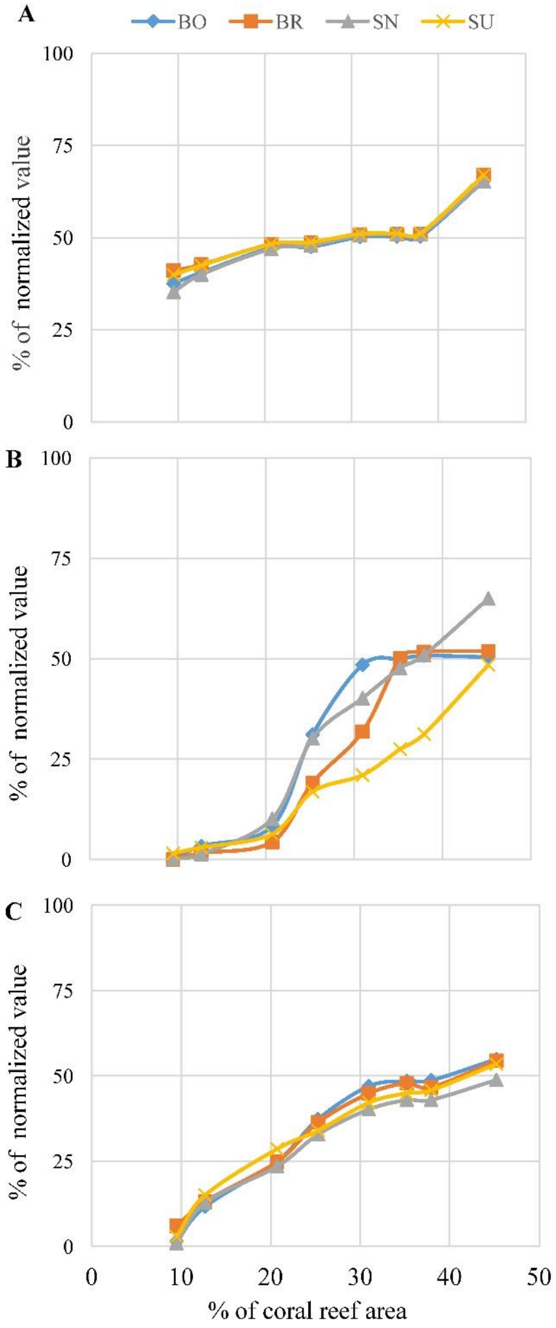

Figure 4.8 Relationship between connectivity, as measured by out-flux (A), betweenness centrality (B), and (C) local retention, and the total reef area selected for conservation. The curves show the percentage of normalised connectivity values for each of the four species: BO denotes the brooder coral, BR the broadcasting coral, SN the snapper, and SU the surgeonfish. The left-hand ends of the curves correspond to scenario 2. The right hand ends of the curves correspond to scenario 1.

4.4 Discussion

Technical constraints and limited ecological data make incorporating connectivity processes into MPA network design a core challenge for conservation science. Theory suggests that habitat connectivity over multiple time-scales might maintain genetic exchange and contribute positively to demographic processes that help maintain the viability of populations and re-establish extirpated ones (Calabrese and Fagan 2004; Minor and Urban 2008). This study demonstrates a tractable approach to incorporating demographic connectivity into a widely used reserve-design tool (Marxan), thereby tackling some of the practical and theoretical challenges involved. The results emphasize that information on habitat quality can substantially alter modelled dispersal patterns. I also illustrate the importance of planning for species with distinct connectivity requirements.

Most previous attempts to integrate connectivity into marine planning have addressed only structural connectivity through automated parameters (Marxan‘s boundary-length modifier) that do not incorporate data on species` dispersal abilities (Magris et al. 2014). Recent applications have developed methods for quantitatively addressing connectivity in relation to spatial dependencies between conservation features (Beger et al. 2010b; Edwards et al. 2010; Jacobi and Jonsson 2011; Lehtomäki and Moilanen 2013; White et al. 2014). The present study builds upon this previous work in several ways. Firstly, I tackled the general question of how to include multiple-species connectivity into planning and tested the common assumption that patch size provides an accurate estimate of reproductive potential in spatially-heterogeneous seascapes subjected to multiple stressors. Secondly, I enhanced MPA design by planning with ecologically-informed connectivity parameters; strong connections between MPAs were achieved with objectives for a range of connectivity measures simultaneously. Finally, I highlighted the conservation gain possible by expanding a network of MPAs beyond the 10% minimal target (10%

being the marine target under the Convention on Biological Diversity – CBD 2013). The approach demonstrates one way of improving the ecological basis of designing MPA networks by increasing the chances of maintaining functional demographic connectivity.

I applied my approach to the case of MPAs to protect coral reefs in Brazil, with reefs represented as a gridded-seascape containing 176 reef cells at 100 km^2 spatial resolution. I used biophysical modelling coupled with Marxan to find MPA configurations guided by connectivity-based metrics. Nevertheless, this framework is flexible and can be adapted to other marine or terrestrial contexts. All three metrics examined here can be readily applied in other seascapes or landscapes, for species for which information on life-history characteristics and habitat distribution is available. Importantly, the approach described here is repeatable in any reserve-design tool that supports planning with threshold objectives. The approach could be implemented, for instance, in Zonation, with its capacity for analyzing data across extensive planning regions with fine resolution data (Moilanen et al. 2011).

4.4.1 The relevance of different life history traits

The findings indicated the locations of geographic barriers that can prevent demographic dispersal of coral-reef species, and identified potential management units for conservation, which might be confirmed through complementary studies of population genetics. I also found considerable differences in connectivity between species: the brooder coral had weaker connections while strongly connected reefs were observed for the surgeonfish. Differences between species in dispersal ability are expected to produce distinct patterns of demographic exchange that are reflected in spatial priorities. The results demonstrate the consequences of not accounting for a range of species with different connectivity abilities in conservation planning: there were substantial mismatches between areas important for achieving connectivity objectives for short-range and long-range dispersers. Hence, a network of MPAs would be expected to have substantial effects in protecting the full suite of species only if their design considered the variety of life-history traits in marine organisms.

The taxa were chosen on the assumption that they were representative of a suite of species. However, marked variations in some biological parameters determining connectivity occur even among species that have similar larval-stage traits or the same reproductive mode. For example, as demonstrated by Rocha et al. (2002), inter-specific differences in salinity tolerance or habitat preferences among adults might change the permeability of barriers between species of Atlantic surgeonfish. While the models are based on the premise that it is possible to derive dispersal ability for a suite of species from taxa representing a particular reproductive strategy, there is a clear need for sensitivity analysis of species-specific life-history traits to determine whether my results can be generalised across other taxa. Further research could also explore how uncertainty around biological parameters used for modelling connectivity influence the selection of places for protection.

4.4.2 Habitat-quality index and connectivity metrics

By investigating the influence of both habitat availability and quality in the number of larvae released, I extended the scope of a previous study by Treml et al. (2012), who determined predictors of broad-scale connectivity in marine populations when quantifying the geographic structure of the dispersal kernel. In my study region, including spatially-heterogeneous habitat quality made a considerable difference to connectivity patterns, indicating the importance of accounting for habitat quality in conservation planning. My approach differed from that of Berglund et al. (2012), who based habitat quality on a stochastic disturbance regime without spatial variance and included only one proxy to determine local growth rate above carrying capacity. My method for estimating habitat quality could be improved by incorporating dynamic disturbances and accounting for synergies between stressors. Using field validation, which is labour-intensive and time-consuming, it might be possible to determine whether the spatial variability of the stressors predicts reef health. For now, though, the use of proxies such as mine can be justified by the known adverse effects of major threats on reproductive output (Minor and Urban 2007; Mouillot et al. 2013) and the need to proceed with conservation decision-making even while the information base is being improved (Pressey et al. 2013).

I identified new opportunities for conserving coral-reef ecosystems in the South Atlantic Ocean in the Abrolhos Bank, the Cape of São Roque, the Cabrália reefs, Itacolomis, and between Camamu and Tinharé. All these areas have high values for out-flux, quality of habitat, local retention, betweenness centrality, and/or a combination thereof. While the Abrolhos Bank is widely regarded as the highest-priority coral-reef area in Brazilian waters, with its high biological diversity and endemism Leao and Kikuchi (2005), other priorities identified in this study either have not been surveyed biologically (Castro and Pires 2001) or are experiencing high rates of environmental deterioration (Kikuchi et al. 2010).

Overall, I found low spatial concordance between high-quality source reefs (i.e., high out-flux reefs; e.g. Abrolhos Bank), self-persistent reefs (i.e. high local retention; e.g. Cape of São Roque reefs), and ecological ‗corridor' reefs (i.e., high betweenness centrality; e.g. northern Bahia reefs), which was likewise noted by Watson et al. (2011b) in the Southern California Bight. The lack of spatial concordance between connectivity metrics can lead to contrasting spatial configurations that optimize either larval local retention or centrality (White et al. 2014 and see also Figure C4.5 in the Appendix C4). Conversely, as demonstrated by Jacobi and Jonsson (2011), the use of joint metrics performs better than single metrics when identifying dispersal links between sites that might be critical to maintain population size and persistence. The differences I found between the responses of distinct metrics in face of constraints on area available for protection support the importance of considering a suite of metrics when analysing the connectedness of potential MPA networks. One way forward is to measure the relative influence of metrics on demographic persistence using metapopulation modelling, which provides insights into balancing the amount of habitat and potential connectivity (see Watson et al. 2011b).

4.4.3 Evaluating the multi-species matrices

While MPAs are usually intended to protect diverse assemblages of species, models that have been used to generate guidelines for MPA design have typically considered single species (Andrello et al. 2015a; Jacobi and Jonsson 2011; Watson et al. 2011b). The use of multi-species matrices combining the functional strategy of each species of interest provides practitioners with a first step toward addressing this problem. Although a similar approach has been taken to integrate population connectivity across species into conservation planning in the Coral Triangle (Treml and Halpin 2012), mine is the first study to determine whether combined connectivity matrices are effective as surrogates for individual species. I showed that, while the MS2 method was generally more effective as a surrogate, it also identified a smaller number of reef cells that were important for the connectivity of all species. This might be a valuable characteristic of a connectivity surrogate in situations with more severe spatial constraints on the extent of MPAs.

I found that multi-species matrices could reasonably represent connectivity for single species for only one metric (out-flux), so might not be fully effective in decision-making about conservation management. My results on the surrogacy value of multi-species matrices were variable, so I could not draw general conclusions about their likelihood of catering for all metrics across species with a variety of dispersal patterns. While I used four candidate species as descriptors of biological assemblages in coral-reef ecosystems, the development of aggregated matrices might be improved by including additional, complementary life-history traits representing other key species of reef habitats (e.g. other reef-building species or fishes at different trophic levels). I also recognize that trophic and competitive interactions among species within communities might complicate the role of dispersal in shaping demographic rates in biological assemblages (Baskett et al. 2007).

4.4.4 Towards a functional approach for incorporating species dispersal into marine conservation planning

Combining the framework described here with other techniques would aid the development of approaches for incorporating connectivity, as an improved proxy for persistence, into the design of MPA networks. This study focused on connectivity across asymmetric and multidirectional dimensions for coral-reef habitats. However, expanding considerations to spatial dependencies across distinct habitats would provide additional insights (see Beger et al. (2010a), Edwards et al. (2010)). Other recent advances have also indicated ways forward. Andrello et al. (2015) accounted for effects of existing MPAs in increasing biological productivity when selecting additions to a reserve network to optimize connectivity and population growth rate. Significant improvements to incorporating connectivity into optimization were demonstrated by White et al. (2014) who compared the performance of reserves using habitat information alone or including single connectivity metrics based on a model of population dynamics.

In the context of this recent work, planning for connectivity in combination with the formulation of objectives for representation, replication, and socioecomics is an important challenge. Little is known about the overlaps and potential trade-offs between aspects of connectivity, representation of multiple habitats and species, and small-scale or commercial fishery objectives. Given the capacity of the conservation planning tool used in my methodological template to deal with tradeoffs and alignments of objectives in a multi-criteria optimization problem (Wilson et al. 2009), the proxies for connectivity can also be combined with information regarding other ecological processes, threats, and costs to embrace a much larger set of objectives in a dynamic context, and account for socio-economic considerations.

A recent review also highlighted the benefits of combining empirical estimates of larval dispersal with biophysical models to ground-truth connectivity patterns and consequently better address the question of how spatial management can maintain the persistence of populations (Burgess et al. 2014). As with all attempts to plan for connectivity, the most appropriate and effective method will rely strongly on complexity of analyses, the assumptions involved in models, and available data. While we are still facing technical or financial obstacles to undertake thorough biological surveys on marine environments, I showed that it would be possible to use hypothetical species for sensibly guiding conservation decisions without a thorough knowledge of species‘ life histories in data-poor regions.

My approach builds on previous work (Magris et al. 2014) showing a progression of approaches from qualitative criteria toward ecologically-informed quantitative objectives. The direction for marine conservation planning with connectivity is moving away from simple rules of thumb for MPA location, size, and spacing (Almany et al. 2009), habitat-specific spacing rules (Anadón et al. 2013), automated parameters in decision support tools that are not species-specific (Beger et al. 2010b), and design based on single connectivity metrics (White et al. 2014). Although I acknowledge recent attempts to select optimum networks of MPAs based on connectivity (e.g. Jacobi and Jonsson (2011), Berglund et al. (2012), (Andrello et al. 2015a), the contribution of my study is to incorporate species with contrasting connectivity abilities and habitat quality into conservation planning tools with the assistance of biophysical modelling and remote sensing. I also showed that the use of combined connectivity matrices for multiple species cannot ensure adequate conservation of all individual species and all metrics. More effective multi-species approaches therefore need to be devised. Finally, I hope that this study might bring connectivity and persistence into ongoing efforts to expand the MPA system off the Brazilian coast.

Chapter 5. Conservation planning for coral reefs accounting for climate warming disturbances[4]

Abstract

Incorporating warming disturbances into the design of MPAs is fundamental to developing appropriate conservation actions that confer coral reef resilience. I propose an MPA design approach that includes spatially- and temporally-varying sea-surface temperature (SST) data, integrating both observed (1985-2009) and projected (2010-2099) time-series. I derived indices of acute (time under reduced ecosystem function following short-term events) and chronic thermal stress (rate of warming) and combined them to delineate thermal-stress regimes. Coral reefs located on the Brazilian coast were used as a case study because they are considered a conservation priority in the southwestern Atlantic Ocean. I show that all coral reef areas in Brazil have experienced and are projected to continue to experience chronic warming, while acute events are expected to increase in frequency and intensity. I formulated quantitative conservation objectives for regimes of thermal stress. Based on these objectives, I then evaluated if/how they are achieved in existing Brazilian MPAs and identified priority areas where additional protection would reinforce resilience. My results show that, although the current MPA system incorporates locations within some of the thermal-stress regimes, historical and future thermal refugia along the central coast are completely unprotected. My approach is applicable to other marine

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ecosystems and adds to previous marine planning for climate change in two ways: (i) by demonstrating how to spatially configure MPAs that meet conservation objectives for warming disturbance using spatially- and temporally-explicit data; and (ii) by strategically allocating different forms of spatial management (MPA types) intended to mitigate warming disturbances and also enhance future resistance to climate warming.

5.1 Introduction

Rapidly increasing concentrations of human greenhouse gases that induce climate change are triggering dramatic declines in coral reefs worldwide (Hoegh-Guldberg et al. 2007). Several factors are thought to be responsible for these declines, including elevated sea-surface temperature, sea-level rise, effects on reef calcification, and solar radiation (Spillman et al. 2011). Increases in sea temperature have led to shifts in species‘ phenologies (Hughes et al. 2010), rates of reproductive success (Baird et al. 2009), metabolic rates (Munday et al. 2009b), and geographic ranges (Hughes et al. 2012). There have also been substantial shifts in the abundance and composition of coral communities affected by bleaching events (Hoegh-Guldberg 1999). In combination with more localised stresses, such as overfishing and degraded water quality, unprecedented thermal-stress disturbances could undermine significant investments in protection of coral reefs over recent decades (Game et al. 2008b). The rapid pace of climate warming is likely to increase damage to coral reefs; consequently, improved understanding of proactive conservation strategies is pivotal to sustainably managing marine populations.

Reef-building corals are particularly vulnerable to rising sea temperatures and are among the most sensitive organisms to climate change (Hoegh-Guldberg et al. 2007). Corals under temperature stress lose the ability to synthesize protective sunscreens, making them more sensitive to sunlight (Hallock 2005). In addition, reef-building corals have relatively long generation times and low genetic diversity, a combination that slows adaptation to environmental changes (Hoegh-Guldberg et al. 2007). Although adaptive responses to thermal stress could increase with climate warming (Logan et al. 2014), adaptive capacity might include a shift to symbiont species with a higher thermal tolerances, which can still be considered a kind of reef degradation (Frieler et al. 2012). Corals already live near their thermal limits (Hoegh-Guldberg 1999). Temperatures that exceed normal summer maxima by only 1°C are enough to cause coral bleaching, and prolonged high temperatures over large areas can lead to extensive mortality (Glynn and D'croz 1990). Disruption of coral growth and composition can also be protracted because rates of recovery vary considerably across species and environmental conditions; such disruption is linked to the recurrence of mortality events, and other concurrent stressors (Baker et al. 2008; Hughes et al. 2003; Linares et al. 2011).

Understanding where and how to mitigate warming disturbances, and thereby manage the resilience of coral reef ecosystems, is a central concern of conservation planning (Mumby et al. 2014). However, conservation plans for coral reefs that account for warming disturbances often neglect the spatial and temporal variability of thermal impacts (Allison et al. 2003; Game et al. 2008b). For example, design of MPAs within the context of climate change frequently uses simple ‗rules of thumb‘, such as selecting multiple, spatially separate samples of the same reef type (replication) to be protected as a risk-spreading approach. (Magris et al. 2014). As a consequence, observations of MPAs mitigating temperature-driven coral loss are limited (Selig et al. 2012). Despite this lack of empirical evidence, MPAs might help to alleviate associated disturbances by removing or reducing non-climate stressors

(Salm et al. 2006), protecting sites that can promote re-colonization of extirpated populations elsewhere (Mumby et al. 2011), or accelerating recovery from uncontrollable disturbances (Bellwood et al. 2004).

Previous studies have suggested a variety of quantitative methods that incorporate thermal-related disturbances into marine planning to design effective strategies for conservation in a changing climate. Most of the prioritization approaches are based on the use of historical satellite data on climate variability (Allnutt et al. 2012; Chollett et al. 2014; Game et al. 2008a; Mumby et al. 2011), predicted climatic regime (Game et al. 2008b), or a combination of both (Levy and Ban 2013; McLeod et al. 2010). However, these studies have not fully integrated historical and predictive climate variability within MPA design tools (but see Levy and Ban (2013)) to identify high-priority areas where coral reefs can be protected both now and in the future. Here, I propose an approach to MPA design that includes explicit spatial and temporal information on warming disturbances to determine spatial configurations of MPAs that meet conservation objectives related to climate change. My approach is applicable when MPAs are designed to simultaneously achieve long-term objectives considering two time frames (historical and future) as opposed to developing MPAs that need to be moved as disturbance regimes shift.

To account for the challenges around MPA design in the context of global warming, the approach described here also offers the opportunity to include a more comprehensive set of management actions than simple generic protection. Rather than focusing only on the dominant approach of protecting areas relatively unaffected by global warming (i.e., thermal refugia, see Ban et al. (2012) and Levy and Ban (2013), I show that MPAs can be strategically located for diverse management actions that also cover sites most suitable for mitigation of cumulative stresses, facilitation of adaptive processes, and future resistance to warming.

This study evaluates the suitability of an MPA system to protect coral reefs under historical and future climate conditions. First, I identify the relative exposures of reefs to different historic and future thermal-stress regimes using measures of chronic and acute stress. Chronic stress corresponds to the long-term rate of warming and can be considered in relation to the ability of organisms to acclimatize (Rezende et al. 2011). Acute stress, occurring over shorter time-scales, can result in sporadic bleaching events that impair ecosystem function (Hoegh-Guldberg 1999). Second, I formulate indicative conservation objectives for thermal-stress regimes that can be set in the decision-making process to boost resilience and aid the development of a climate-resilient MPA system. Finally, I assess the gaps in the representation of thermal-stress regimes by an existing MPA system and identity priority areas where additional protection would capture complementary thermal-stress regimes, thereby reducing the risk of establishing climatically unrepresentative reserves.

5.2 Materials and Methods

My study comprised a three-step procedure for incorporating potential warming disturbances into MPA design, using detailed information on historical and future thermal stress (Fig. 5.1). The steps were: (A) data collation, (B) selection and calculation of metrics of thermal stress, and (C) incorporation of warming disturbances into marine conservation planning. The method considered both the magnitude and duration of climate-related exposure to stress and the ability of coral reefs to withstand such exposure. I included historical data (henceforth referred to as ‗observed‘ data) and future projections of climatic conditions (henceforth referred to as ‗projected‘ data) because I aimed to analyse not only those areas that have already experienced changes but also those most likely to be affected by future climate-related disturbances.

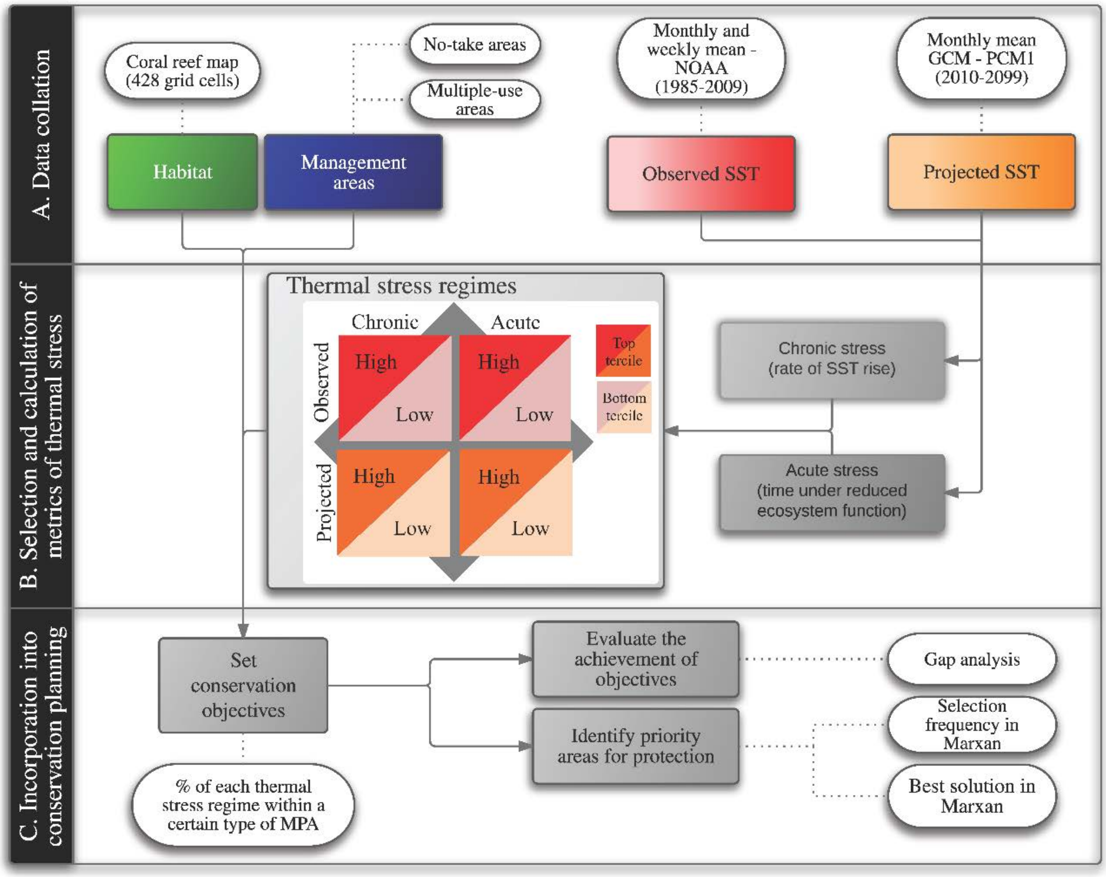


Figure 5.1 Methods of this chapter divided into three major phases. (A) Data collation involved acquisition of habitat data (green box), boundaries of marine protected areas (MPAs) (blue box), and observed and projected data (red and orange boxes, respectively) on sea-surface temperature (SST). In the selection and calculation of metrics of thermal stress (B), I derived metrics of chronic and acute stress from observed and projected datasets and combined them to define thermal-stress regimes. Regimes were delineated based on upper and lower terciles labelled as "high" (highest 33% of values, dark red or orange) and "low" (lowest 33% of values, light red or orange), respectively. The incorporation of warming disturbances into conservation planning (C) consisted of setting conservation objectives for each thermal-stress regime, evaluating their achievement in existing MPAs, and identifying priority areas that would achieve unmet objectives. Arrows in gray indicate the flow of information and lighter boxes linked by dashed lines depict types of data or analyses involved in each step.

The study area covers Brazilian coral reefs (within ~4º30'N – 51º37'W to ~18º30'S – 24º38'W), which are a priority for marine conservation in the southwestern Atlantic Ocean. In Brazil, warming temperatures appear to be driving both coral bleaching (Leão et al. 2010a) and the incidence of coral diseases (Francini-Filho et al. 2008). Bleaching events have been recorded predominantly on the eastern reefs (Bahia state) since 1993 (Leão et al. 2008); there is a paucity of field data on bleaching in other areas (but see (Amaral et al. 2006; Ferreira et al. 2013)). In the years in which major events occurred (1997/1998, 2002/2003, 2009/2010), bleaching was fairly widespread, spanning about 500 km of coast, and causing significant coral mortality and/or sublethal effects (Kelmo et al. 2003; Leão et al. 2010a; Miranda et al. 2013). Although Brazilian reefs are thought to conform only partially with global patterns of bleaching (Leão et al. 2008) sea temperature has been identified as a key driver of bleaching events (Krug et al. 2013). Despite high relative representation of Brazilian coral reefs within MPAs (Magris et al. 2013), reef degradation has not been mitigated or prevented by local management (Ferreira et al. 2013; Gerhardinger et al. 2011).

5.2.1 Data collation

The total area of coral reefs in Brazil is ~900 km^2 occurring in three distinct geographical sectors: northern, central, and southern (Fig. 5.2A). To align with the temperature data (see below), I identified ~4 x 4 km grid cells that contain coral reefs (habitat data). The resulting 428 reef cells were used to summarize results for thermal stress and selection of potential new MPAs. I also compiled a dataset on existing MPAs along the Brazilian coast (Fig. 5.2A) with their legal boundaries (Magris et al. 2013). Here, I refer to an MPA system as an array of individual MPAs encompassing a wide range of management types and levels of protection. For the purposes of this study, I consider two management types: (i) no-take areas, where ecosystems should be preserved in a state undisturbed by extractive activities; and (ii) multiple-use areas, with objectives to promote the sustainable use of the marine environment by a wide variety of users, with extractive activities permitted but regulated.

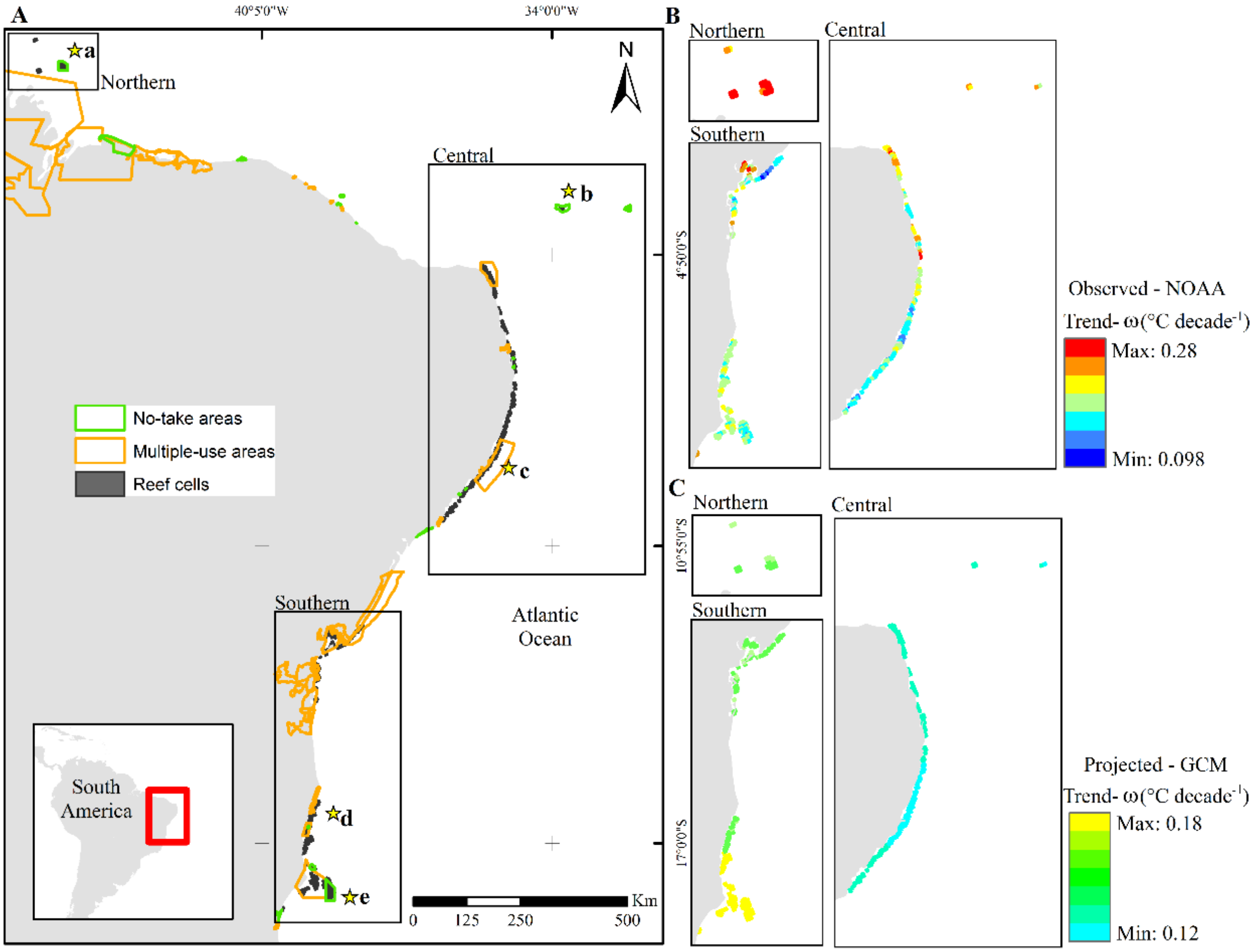


Figure 5.2 The study area and the chronic stress metric. (A) Sectors (northern, central, southern), reef cells (n=428), and the existing MPA boundaries along the Brazilian coast. MPAs are classified according to their main management categories: no-take areas and multiple-use areas. Letters a-e with stars denote approximate locations of reef cells selected to depict temperature variability (see Figure 5.6). (B) Decadal SST trends describe observed chronic stress for each reef cell from NOAA satellite data. (C) Decadal SST trends describe projected chronic stress for each reef cell, downscaled from PCM1 general circulation model output.

For historical analysis, I acquired data on sea-surface temperature (SST) from the National Oceanic and Atmospheric Administration (NOAA) Pathfinder Project (http://pathfinder.nodc.noaa.gov) (Casey et al. 2010). Version 5.0 data at ~4 km spatial resolution spanning the period 1985–2009 were retrieved for my study area. The dataset comprised a lengthy, accurate, and consistent set of records with high spatial resolution (Casey et al. 2010). The information in these records has contributed to a wide range of marine applications related to conservation (Chollett and Mumby 2013; Halpern et al. 2008; Maina et al. 2008). I used only night-time values because they are most relevant for coral habitats (Heron et al. 2013). Weekly composites of only high-quality values were produced and data gaps filled, following the method of Heron et al. (2010).

For my analysis of future projections, I used global monthly SST output (2010-2099) by the Parallel Climate Model PCM1, which is a General Circulation Model (GCM) developed by the National Center for Atmospheric Research (NCAR) for the Intergovernmental Panel on Climate Change, Fourth Assessment (IPCC AR4). PCM1 outputs were acquired from the World Climate Research Program Coupled Model Intercomparison Project Phase 3 (WCRP CMIP) multi-model database. The model has an oceanic resolution of ⅔° ½° and has the lowest climate sensitivity (1.7 °C) among the 23 different IPCC models that predict disturbances of climate change on ocean temperature (McAvaney BJ 2001). This model was selected because it represents a lower bound for projected ocean warming and has performed relatively well in a global prediction of bleaching frequency (Donner et al. 2005). The output files were selected for the A1B emission scenario, which represents business-as-usual greenhouse gas emissions over the current century; under this scenario, atmospheric concentration of greenhouse gases will reach 720 ppm by 2100 and stabilize at this level. The scenario describes increases in concentration of greenhouse gases attributable to expected human population growth and industrial development. A1B scenarios are mid-line within the A1 scenario family for carbon dioxide output and economic growth (Nakicenovic et al. 2000).

A key limitation revealed by spectral analysis is that many GCMs under- or over-represent variability about their means (the baselines from which predictions are produced) or seasonal cycles, reducing their capacity for projections of coral bleaching (van Hooidonk et al. 2014) and for undertaking more informed conservation planning (van Hooidonk et al. 2015). Importantly, van Hooidonk and Huber (van Hooidonk and Huber 2012) detected PCM1 over-prediction of some components of climate, such as the variability of the tropical ocean seasonal cycle and ENSO in a comparison with observations of SST data averaged over all global reef locations. Recognizing this limitation in attempts to realistically represent SST variability and accurately predict bleaching for some of my reef locations, I applied a bias-removal technique following the method described by Dunne et al. (2013) to make the forecasts more consistent in intensity and timing (Appendix C5). This involved statistical downscaling of the coarse spatial resolution of the GCM projections to the fine resolution of historical satellite data (~4 km) and included setting the mean and variance of the projections to those of the observational data (using retrospective projections covering 1985-1999, i.e. the training period; see Fig. C5.1 in Appendix C5) (Dunne et al. 2013). Although the downscaling process performed here does not resolve local-scale features such as eddies, high-resolution (4 km) observations and projections of SST are suitable for MPA design and management (van Hooidonk et al. 2015).

While other observed and projected datasets have since become available, the SST datasets described above were the most-recently available at the time of analysis.

5.2.2 Selection and calculation of thermal stress metrics

Myriad measures of thermal stress could be used in marine conservation planning as predictors of coral-reef resilience in the face of climate-related disturbances (Ban et al. 2012; Donner 2009; Donner et al. 2007; Game et al. 2008b; Levy and Ban 2013; Liu et al. 2006; Maina et al. 2008; Maynard et al. 2008; McLeod et al. 2010; Selig et al. 2010, 2012). Two indicators – SST trend and Degree Heating

Weeks (DHWs) – emerged from previous studies as realistic and reliable ways of detecting detailed spatial and temporal patterns in disturbances of temperature on coral-reef ecosystems (Chollett et al. 2012; Liu et al. 2006). SST trends and DHWs were used to determine the spatial distribution of chronic and acute thermal stress, respectively, across my study area. These metrics allowed me to accurately compare different thermal-stress regimes based on both observed and projected SST datasets (Fig. 5.1B).

Chronic thermal stress

Chronic thermal stress was measured as the estimated rate of SST warming following Chollett et al. (2012) and Weatherhead et al. (1998). Observed data were composited to monthly resolution (from weekly) for calculation of trends. I used non-linear mixed effect models (package nlme in R) because they are among the most robust statistical models for the detection of reliable trends in SSTs (Chollett et al. 2012) and are widely used to detect trends in environmental data (Good et al. 2007; Zhang and Reid 2010). The basic structure of the model is:

$$SST_t = \mu + S_t + \omega t/12 + N_t \qquad (5.1)$$

where, SST_t at a given time t (in months) is a function of a constant term μ, a seasonal component S_t, a linear trend ω of the rate ℃ yr^{-1} and residuals N_t, which is an assumed autoregressive of order one (AR-1 autocorrelation form). This structure allowed me to account for some variability in the time series, such as seasonality and serial correlation, which influence the magnitude and significance of the calculated trends (Weatherhead et al. 1998). By using monthly means derived from satellite observations and GCM outputs, I quantified the overall trend in SST (in ℃ $decade^{-1}$) to estimate long-term, chronic thermal stress in both observed and projected data for each reef cell.

Acute thermal stress

Acute thermal stress was based on DHWs, a well-established indicator of coral bleaching that combines both intensity and duration of warm anomalies in relation to ecological thresholds (Eakin et al. 2010). Empirical evidence indicates a strong relationship between bleaching / mortality and level of heat stress: some coral bleaching is predicted to occur when the DHW value exceeds 4 °C-weeks; widespread mortality is expected when it reaches 8 °C-weeks (Eakin et al. 2010). I assessed both spatial distribution of annual maximum DHW and number of bleaching-level stress events (DHW ≥ 4 °C-weeks) per decade. Reef recovery, and the sustained provision of various ecosystems goods, might not occur when two or more bleaching-level events occur per decade (Connell et al. 1997; Sheppard 2003).

DHWs were derived from two sources: (1) observed: weekly composites of satellite SST data, and (2) projected: monthly mean SST from PCM1 outputs. I calculated observed DHWs by taking the sum of the positive SST anomalies that exceeded the maximum climatological temperature (warmest long-term monthly average) by at least 1 ℃ through a 12-week window (Liu et al. 2006; McLeod et al. 2010). I subsequently recorded annual maximum DHWs for each reef cell to provide the basic historical metrics of acute stress.

To predict the occurrence of acute coral bleaching events in the period 2010–2099, I first calculated Degree Heating Months (Donner et al. 2005) by summing positive modelled SST anomalies compared with the maximum monthly SST provided by satellite climatology (cf. Donner et al. (2007)) through a three-month rolling window. Annual maximum DHM values were recorded for all grid cells and converted into DHWs (using the relationship in Donner et al.(2009)).

I sought to characterize a single value for acute disturbance at each reef cell that took into account both frequency and intensity of bleaching-level stress events through each record. Summing individual values for thermal exposure through the time-series would not distinguish between the dramatic difference to ecosystem disturbance from infrequent severe events (e.g., three events with DHW of 6 °C-weeks, totaling 18 °C-weeks) as compared with frequent moderate events (e.g., nine events with DHW of 2 °C-weeks, also totaling 18 °C-weeks). I developed a logistic function model to estimate the amount of time a given reef cell is under reduced ecosystem function (capacity to grow, repair, and reproduce) after each discrete disturbance event based on DHW values (t_c in Fig. 5.3). Values of t_c are short after exposure to low DHW values: natural communities are highly resilient to disturbance under low levels of stress and corals would move back to a natural steady state quickly (Bellwood et al. 2004). The response of t_c then increases rapidly from the onset of bleaching-level stress (DHW = 4 °C-weeks; Eakin et al. (2010)). At this level, selective mortality following disturbance has a direct impact on the structure and composition of the coral community, by changing the absolute and relative abundances of coral species and filtering out less tolerant species (Hughes and Connell 1999). As further thermal disturbance degrades the ecosystem and colonies are decimated over large spatial scales, the function flattens because only species with stress-tolerant life histories are present. The function then reaches an upper bound where no additional time is needed as acute thermal stress has extirpated all organisms. This model represents the conventional view of resilience (see Bellwood et al. (2004)) and provides a realistic relationship between acute stress events and recovery of ecosystem function *ceteris paribus*.

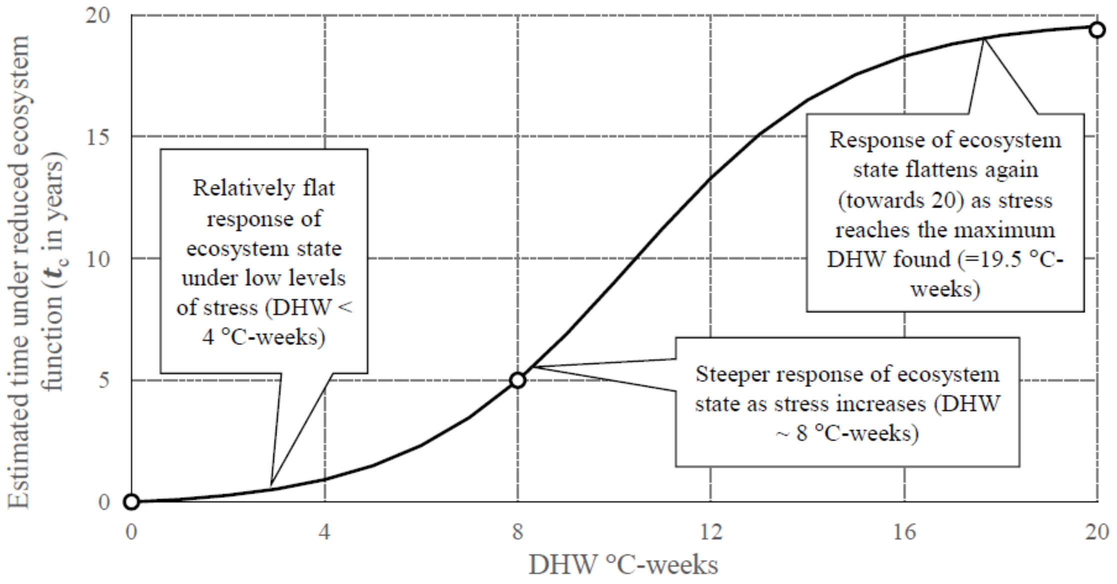


Figure 5.3 Conceptual illustration of the effects of acute thermal stress on coral-reef ecosystem state described by a logistic function. Empty circles indicate values used to fit the model. The form of this function assumes that the time that coral reefs spend with reduced ecosystem function (capacity to grow, repair, and reproduce), t_c*, is short at low DHW values because I expect that corals would recover quickly (within one year). This is followed by a steeper increase in* t_c*; when widespread mortality begins (DHW reaches 8 °C-weeks), the time that corals would spend recovering increases rapidly as bleaching-level events intensify above this level. When almost the entire community is extirpated over large spatial scales (above about 16 °C-weeks), I expect to have small increments of* t_c *with increasing DHW for the ecosystem as a whole because only stress-tolerant species that can withstand greater acute disturbance are present. When almost the entire community is extirpated over large spatial scales (above about 16 °C-weeks), I expect to have small increments of* t_c *with increasing DHW for the ecosystem as a whole because only stress-tolerant species that can withstand greater acute disturbance are present. The function then reaches an upper bound (i.e., in the formulae - asymptotic value - equal to 20 years) which is the maximum time required to regenerate a fully functional ecosystem after bleaching causes massive mortality and extirpates all organisms.*

Scientific evidence indicates that coral reefs that have experienced severe acute events with high associated coral mortality (DHW = 8 °C-weeks) require at least 5 years to shift back to their original condition; 20 years is defined as the longest period required for returning to an unaltered state once coral mortality has resulted in complete degradation of the reef ecosystem (Baker et al. 2008; Connell et al.

1997; Golbuu et al. 2007; Sheppard 2003) and coincides with the maximum DHW found. I used this information to empirically fit the logistic function:

$$t_c = \frac{c}{1+ae^{-bx}} + d \quad (5.2)$$

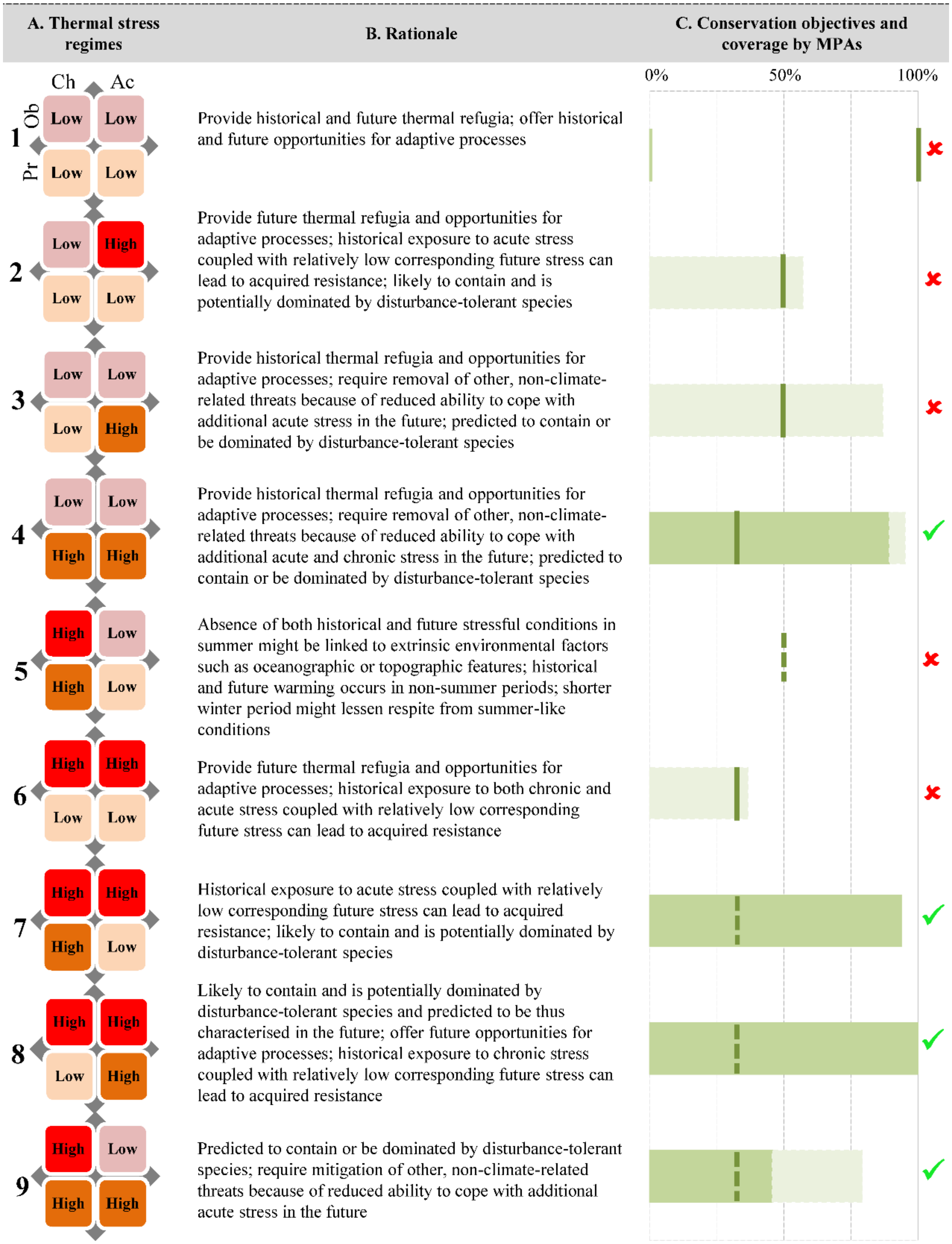
where t_c is the estimated time under reduced ecosystem function following exposure to annual maximum DHW of x for each year; a, b and c are parameters; and $d = -c/1 + a$. The values for controlling parameters a and b were determined by an experimental curve-fitting procedure and c was the asymptotic value or the maximum observed time to fully shift back to unaltered state after bleaching caused massive mortality.

The acute stress metric accumulated the function values above to calculate the total amount of time that a given reef cell would spend recovering from acute events with reduced ecosystem function across each of the observed and projected time series as an estimation of total disturbance from past and future short-term events, respectively. This employed an assumption that each subsequent acute event contributed additively to reef degradation, regardless of how close to full recovery a given grid cell might be since the prior acute disturbance. Importantly, the underlying concept of my metric does not take into account any adaptation or acclimation by corals and their symbionts to increasing thermal stress. Accordingly, the metric is a pessimistic estimate of the amount of time in which each reef cell was prevented from returning to its unaltered state. Values are presented as number of years per decade, allowing direct comparison between observed and projected indices.

5.2.3 Incorporating warming disturbances into marine conservation planning

Thermal-stress regimes

I began this exercise by partitioning the planning region into distinct disturbance regimes. For this step, metrics of both chronic and acute thermal stress were normalised to range between zero and one, where one reflected the maximum value across all reef cells throughout each data set (observed and projected). Thus, I produced four single values of stress for each reef cell (Fig. 5.1B). Disturbance regimes were delineated by identifying reef cells that fell within the upper and lower terciles of each stress measure calculated for the two time series. Upper and lower terciles (labeled as ―high” and ―low”) were chosen because reef cells attributed to those values were generally subjected to the most or least disturbances to natural ecosystems (Yang et al. 2012). To this end, each of the 428 reef cells (planning units) was allocated either to one of the 16 possible disturbance regimes or left uncategorised if the cell had any of the four values in the middle terciles. Of the 16 potential combinations, nine thermal-stress regimes were present in the study area and considered for management attention (Fig. 5.4A and B).



A. Thermal stress regimes	Ob Ch	Ob Ac	Pr Ch	Pr Ac	B. Rationale	C. Conservation objectives and coverage by MPAs
1	Low	Low	Low	Low	Provide historical and future thermal refugia; offer historical and future opportunities for adaptive processes	✗
2	Low	High	Low	Low	Provide future thermal refugia and opportunities for adaptive processes; historical exposure to acute stress coupled with relatively low corresponding future stress can lead to acquired resistance; likely to contain and is potentially dominated by disturbance-tolerant species	✗
3	Low	Low	Low	High	Provide historical thermal refugia and opportunities for adaptive processes; require removal of other, non-climate-related threats because of reduced ability to cope with additional acute stress in the future; predicted to contain or be dominated by disturbance-tolerant species	✗
4	Low	Low	High	High	Provide historical thermal refugia and opportunities for adaptive processes; require removal of other, non-climate-related threats because of reduced ability to cope with additional acute and chronic stress in the future; predicted to contain or be dominated by disturbance-tolerant species	✓
5	High	Low	High	Low	Absence of both historical and future stressful conditions in summer might be linked to extrinsic environmental factors such as oceanographic or topographic features; historical and future warming occurs in non-summer periods; shorter winter period might lessen respite from summer-like conditions	✗
6	High	High	Low	Low	Provide future thermal refugia and opportunities for adaptive processes; historical exposure to both chronic and acute stress coupled with relatively low corresponding future stress can lead to acquired resistance	✗
7	High	High	High	Low	Historical exposure to acute stress coupled with relatively low corresponding future stress can lead to acquired resistance; likely to contain and is potentially dominated by disturbance-tolerant species	✓
8	High	High	Low	High	Likely to contain and is potentially dominated by disturbance-tolerant species and predicted to be thus characterised in the future; offer future opportunities for adaptive processes; historical exposure to chronic stress coupled with relatively low corresponding future stress can lead to acquired resistance	✓
9	High	Low	High	High	Predicted to contain or be dominated by disturbance-tolerant species; require mitigation of other, non-climate-related threats because of reduced ability to cope with additional acute stress in the future	✓

Figure 5.4 Thermal stress regimes. The nine thermal-stress regimes defined within the study area (A), defined by combinations of high and low values for observed (Ob) and projected (Pr) chronic (Ch) and

acute (Ac) stress. The rationale for management of each regime is summarised in (B). (C) Conservation objectives (dark green vertical lines) for each thermal-stress regime and their coverage by MPAs (green bars). Objectives prescribe the percentage of the total extent of reef cells in the regime (100%, 50%, or 30%) requiring management and the type of management required (no-take – solid green lines; multiple-use areas – dashed green lines). Horizontal bars indicate the percentage of each thermal-stress regime covered by the two types of MPAs: no-take MPAs are indicated by green bars; multiple-use MPAs are indicated by light green bars. The symbol "✓" indicates that the conservation objective has been fully achieved in both extent and management type; "✗" indicates that the conservation objective has not been attained. Objectives were formulated for explictiness in the design of MPAs to account for resilience to warming disturbances, considering supporting evidence in the literature (see Fig. C5.2 in Appendix C5 for further details about rationales to protect all regimes).

Prioritisation approach

To select priority areas for marine conservation, thereby enhancing my ability to promote resilience in a warming and uncertain future, I aimed to design an MPA system that addressed dynamic features of a seascape, such as the full range of thermal-stress regimes (see Fig. 5.4A and 5.4B for regime definitions and Appendix C5 for detailed characteristics). This approach targets areas that: (i) have relatively stable historical and/or future climates and are least affected by sporadic events (areas that are historical and/or future thermal refugia, and hence enhances species‘ likelihood to persist) (regimes 1-4, 6); (ii) offer historical or future opportunities for increasing the capacity of species to respond to temperature rise through adaptive processes (regimes 1-4, 6, 8); (iii) do not experience stressful conditions in summer, both historically and in the future, which might be linked to extrinsic environmental factors such as oceanographic or topographic features, and prevent mortality (regime 5); (iv) are likely to have developed resistance given prior exposure to acute and/or chronic stress, coupled with relatively low corresponding future stress, which might maintain survival (regimes 2, 6-8); (v) require removal or mitigation of non-climate-related threats because of reduced ability to cope with additional chronic and/or acute stress in the future (regimes 3, 4, 9); (vi) are characterised by historical and/or future warming in non-summer periods, with reduced winter respites from summer-like conditions and make ecosystem more resistant or resilient to bleaching-stress events (regime 5); and (vii) are most likely to contain and are potentially dominated by disturbance-tolerant species and/or predicted to be thus characterised in the future, and can boost resilience to warming disturbances (regimes 2-4, 6-9).

Using the systematic conservation tool Marxan, I selected reef cells to achieve the conservation objectives for the nine regimes (Fig. 4C). To formulate the conservation objectives, I reviewed recommendations from twelve papers (Ban et al. 2012; Côtê and Darling 2010; Hansen et al. 2010a; Heron et al. 2010; Keller et al. 2009; McCook et al. 2009; McLeod et al. 2009; Selig et al. 2010, 2012; van Hooidonk et al. 2015; West and Salm 2003); see Fig. C5.2 in Appendix C5), offering guidelines for management of coral reefs under climate change or proposing methodological frameworks with conservation implications. I then used a decision tree to derive specific management requirements translated into quantitative objectives (Fig. 5.5).

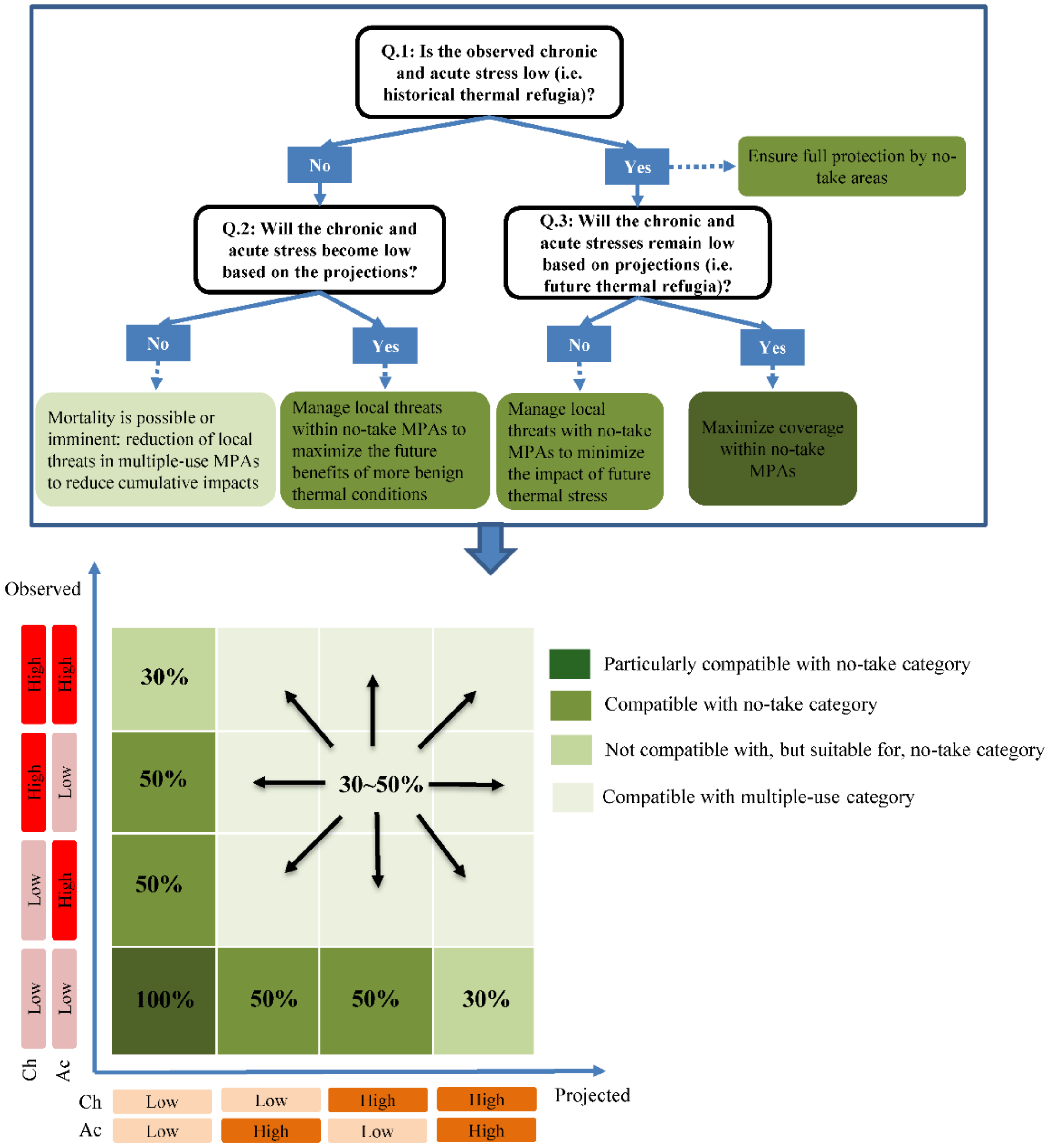


Figure 5.5 Decision tree for using information on chronic and acute stress derived from observed and projected data to formulate quantitative conservation objectives for warming disturbances. Ch = chronic stress, Ac = acute stress. Percentage values inside boxes in the bottom of the figure are prescribed (but indicative here) coverages by no-take and multiple-use MPAs.

The suggested management type for achievement of objectives was defined by considering the historical or future ecosystem state in each regime. For example, areas that have experienced low levels of observed thermal stress or are projected to experience least future stress could retain naturally-functioning ecosystems, and should be more strictly protected (no-take MPAs). Conversely, reef cells that experienced high observed thermal stress or are projected to experience future stress might indicate some level of environmental degradation and are allocated within multiple-use MPAs. For thermal-stress regime 1 (see Fig. 5.4C), the conservation objective was 100% of coverage within no-take areas, but objectives for other regimes are either 30% or 50%. The assignment of the MPA type to meet the conservation objectives was implemented as a *post-hoc* analysis and had no influence on the selection of priority areas in Marxan. The conservation objectives are indicative and will need to be refined adaptively as knowledge accumulates on the management requirements of regimes.

Spatial prioritization in Marxan was repeated 100 times, and final conservation planning scenarios were obtained after 10 million iterations. I set a high penalty value to each thermal regime to ensure that all objectives were fully achieved. I ran two scenarios, one ignoring existing MPAs to identify their coincidence with areas selected at lowest possible cost (measured in this case by total area of reef cells) and one mandating protection for the existing MPAs, and therefore serving as a gap analysis (Fig. 5.1C). For the second scenario, the reef cells coinciding spatially with existing MPAs ($n = 60$) were locked in for the analyses. For both scenarios, I recorded the best solution and selection frequencies of reef cells.

5.3 Results

5.3.1 Chronic thermal stress

The observed and projected SST patterns identified an overall warming trend throughout the study area; there were no instances of observed nor projected of cooling trends (Fig. 5.2B and C). To illustrate variations in SST characteristics, I selected five reef cells (shown in Fig. 5.2A) within different thermal-stress regimes (Fig. 5.6). Across the historical time series, warming rates ranged from 0.098 °C to 0.280 °C decade^{-1} (average: 0.19 °C decade^{-1}). Compared with observed satellite data, the projected rate of SST rise was slower through the 21st century PCM predictions (Fig. 5.2C), and the range of projected trend values was smaller than observed ones within the study area (from 0.12 to 0.18 °C decade^{-1}; average: 0.15 °C decade^{-1}). However, it is notable that the time period through which trends were calculated differed nearly four-fold. While recent trends could accurately represent longer-term historical trends, they might also be influenced by ocean variabilities of multidecadal periodicity (e.g., the Atlantic Multidecadal Oscillation, 60-70 year period, (Kerr 2000)) that, depending on the phase through the calculation period, can enhance or diminish the short-term trend.

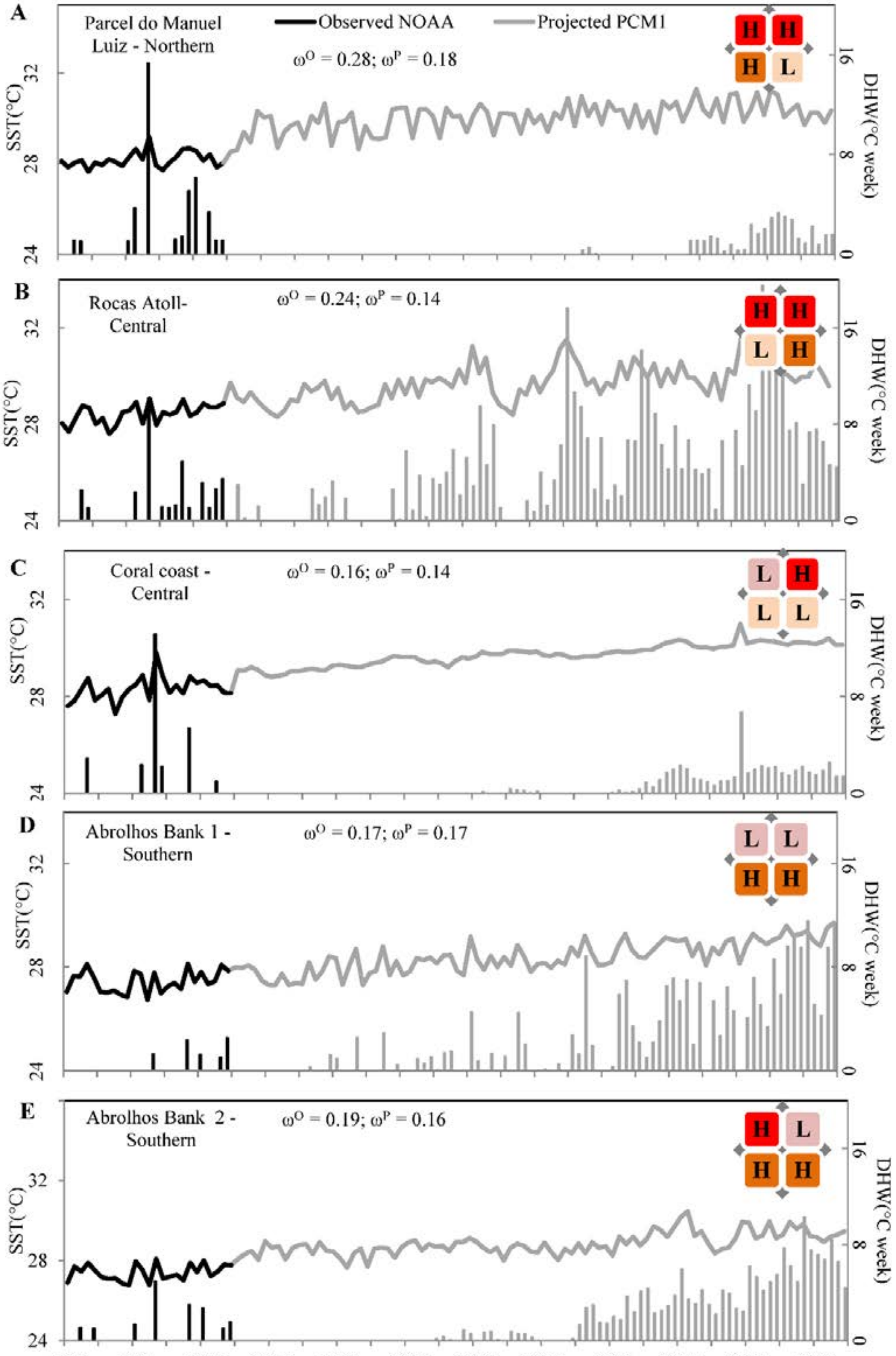


Figure 5.6 Annual maximum SST and Degree Heating Weeks (DHWs) for five reef cells within different thermal-stress regimes. Approximate locations of the five cells are shown as a-e in Fig. 5.2A. Observed

data (satellite NOAA) are shown by black solid lines (SST values) and filled bars (DHWs) while projections (GCM PCM1 output) are shown by gray solid lines (SST values) and filled bars (DHWs). Warming trends (in °C per decade) are shown for observed (ϖ^O) and projected (ϖ^P) time series. The thermal-stress regime allocated to each reef cell is indicated in the top right of each graph, and defined in Fig. 5.3.

Although SST rose most rapidly in reefs closer to the equator (Figs. 5.2B and 5.6A), reefs situated further south and in the central of the study area (Figs. 5.2B and 5.6B-E) also warmed quickly. Projected warming was more pronounced over the southern and northern reef cells than in the central sector. Even after suppressing SST variance associated with year-to-year variability induced by the ENSO cycle and seasonal variability, I detected greater variability in the most northern and southern reefs in the study area (Fig. 5.6). Only 6.3% of the reef cells (all from the southern sector) had projected warming rates greater than observed trend.

5.3.2 Acute thermal stress

While projected warming rates in the future were lower than in recent historical data, an increase in the acute stress metric associated with bleaching-level stress events was evident for many reef cells located in the central and southern sectors (Fig. 5.6 and 5.7). Nearly 45% of reef cells were projected to face a greater proportion of time under reduced ecosystem function following acute events than historically observed. Accumulated time under reduced ecosystem function across reef cells ranged from 0.6 to 10.0 years decade^{-1} for the observed time series (average: 1.93 years decade^{-1}) and from 0.3 to 10.0 years for the projected GCM model (average: 2.59 years decade^{-1}). Most reef cells had annual maximum DHW values exceeding 4 °C-weeks in at least one year of both datasets (87% and 82% of reef cells in the observed and projected time series, respectively) over the whole planning time window (Fig. C5.3 in Appendix C5). The observed data indicated that only 3.9% of reef cells had been exposed to two or more bleaching-level events (DHW exceeding 4 °C-weeks) per decade, but inferences from PCM model output indicate that 28% of reef cells were projected to exceed this event frequency (Fig. C5.3 in Appendix C5).

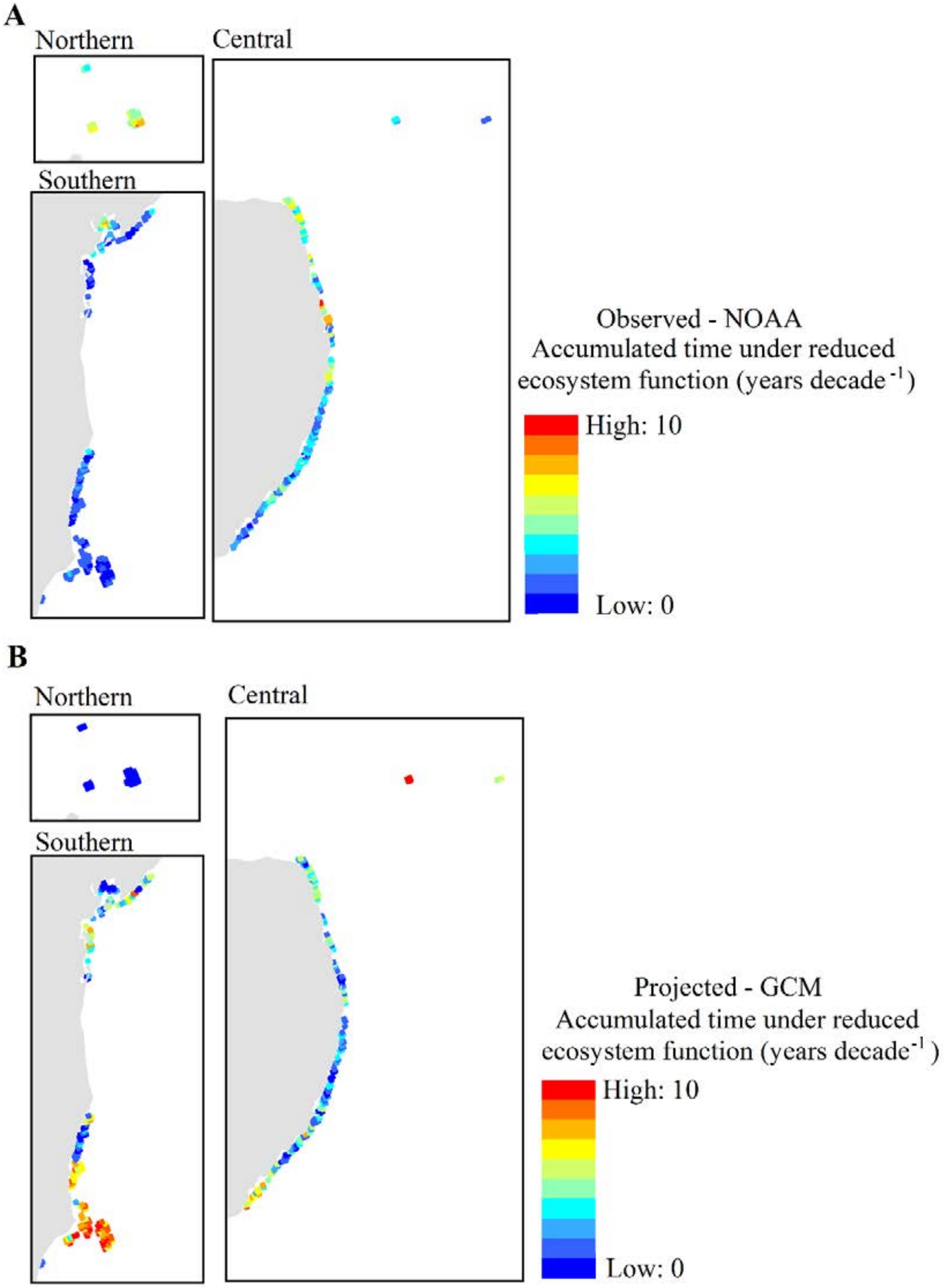


Figure 5.7 The acute thermal stress metric. Accumulated time for which the ecosystem is under reduced ecosystem function from acute stress events for all reef cells according to observed (A) and projected (B) time series. Ccc Times are derived from the logistic function used to relate intensity of acute stress

events to recovery time (Fig. 5.3) and summed through each time-series and presented as years per decade. Panels for reefs in the northern, central, and southern sectors of the study area correspond to insets in Fig. 5.2A.

The acute stress metric through the observed data shows a spatial pattern of increased values towards the northern sector (Fig. 5.7A). In contrast, reefs in the southern are projected to experience the greatest time under reduced ecosystem function in the future (Fig. 5.7B). An exception to this general pattern is projected for the Rocas Atoll (offshore in the very north of the central sector, see also Fig. 5.6B), where the most severe projected stress (19.4 °C-weeks) will exceed that experienced historically (10.0 °C-weeks). Southern reefs are projected to experience the greatest time under reduced ecosystem function because they are almost the only ones to have bleaching-level stress events exceeding the suggested threshold of two events per decade and thus leading to reef degradation (Fig. C5.3 in Appendix C5). In contrast, northern reefs are projected to maintain event frequencies similar to that recently observed through the remainder of the century (Fig. C5.3 in Appendix C5). Rocas Atoll is exceptional again because disturbances are predicted to occur at a rate approaching five per decade.

5.3.3 Thermal-stress regimes and conservation objectives

Approximately 24% of reef cells (101 of 428) fell within one of the nine thermal-stress regimes, the remaining cells having middle-tercile values for at least one of the four variables used to classify regimes. Descriptive statistics for all metric values used to formulate regimes are shown in Table C5.1 (Appendix C5). The cells allocated to regimes were distributed across all three sectors of the study area (Fig. 5.8A). The most extensive regimes occurred in those areas subjected to recent bleaching-level stress events but with increased potential ability to survive future stress (high observed acute stress and low projected acute stress). These were regimes 2, 6, and 7, accounting for about 56% of the total reef cells assigned to regimes (Fig. 5.8A and B). Examples of these regimes were mostly located on isolated reefs and near-shore banks off the coast in the central sector. Regimes that require management at local scales to avoid increased mortalities resulting from non-climate-related threats were also well represented. These regimes (3, 4 and 9) accounted for about 39% of all allocated reef cells (Fig. 5.8A and B). These regimes were mostly represented in the southern sector and included the outer reef arc in the Abrolhos region. Only 2% of assigned reef cells were in regime 1, with minimal disturbances from observed and projected chronic and acute stress (Fig. 5.8B). These historical and future thermal refugia were inshore isolated bank reefs located off the central coast (Fig. 5.8A). Areas projected to have higher rates of coral mortality from future acute stress, and therefore requiring local management interventions to mitigate disturbances, include bank reefs forming the coastal arc of the Abrolhos Bank and the Rocas Atoll (regimes 4, 8 and 9 in Fig. 5.8A).

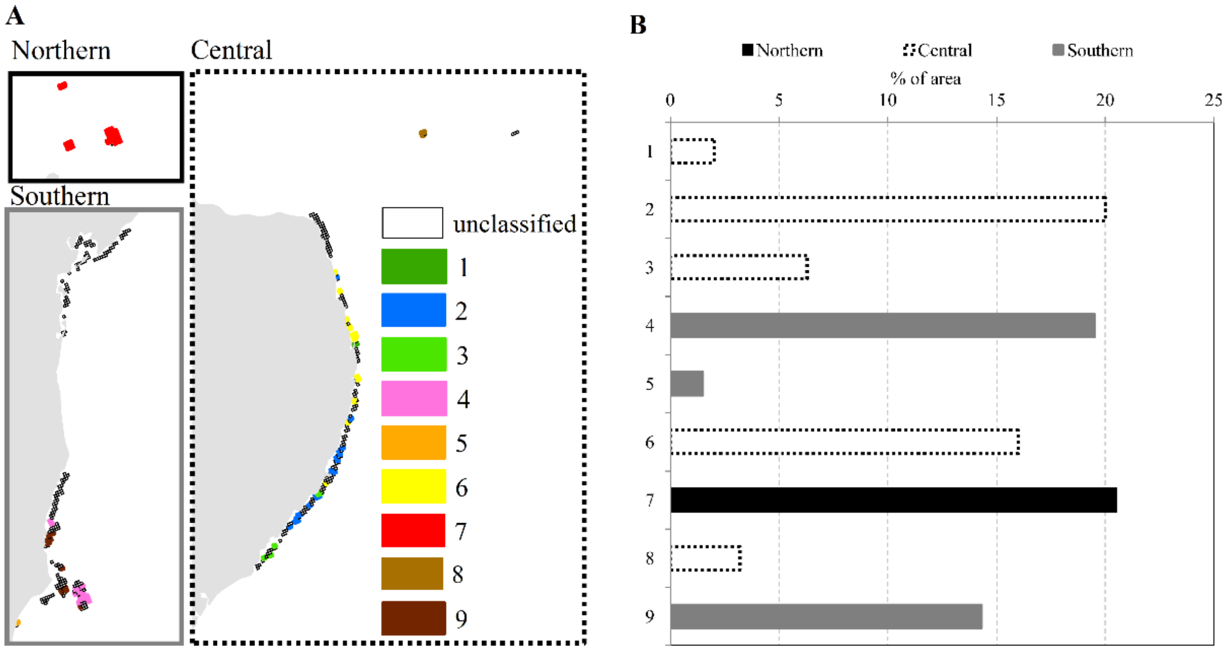


Figure 5.8 Distribution of thermal-stress regimes across study area. (A) Reef cells to which the nine regimes were allocated. Empty (black outlined) cells are unclassified because they have middle-tercile values for at least one of the four variables used to classify regimes. Labels for thermal regimes match those in Fig. 5.4. Views for reefs in the northern, central, and southern sectors correspond to insets in Fig. 5.2A. (B) Areal coverage of each thermal-stress regime as a percentage of the total of all reef cells allocated to regimes (n=101). Each regime was encapsulated within a single sector.

The current MPA system achieved four of the nine conservation objectives (Fig. 5.4C) considering both coverage and type of management. There were substantial shortfalls in achieving objectives for historical and/or future thermal refugia (regimes 1, 2, 3 and 6). Although regime 3 occurred widely in multiple-use areas (>80% of these areas), the objective for this regime was 50% coverage by no-take zones. A key finding of my gap analysis was that many regimes that could be managed inside multiple-use areas (less restrictive types of MPAs) achieved their objectives through coverage by no-take zones (Fig. 5.4C).

Requiring that existing MPAs be selected in the spatial prioritization analysis identified 16.8% of reef cells (72 of 428) to achieve the prescribed objectives (Fig. 5.9A). All but twelve of these cells were in existing MPAs; however, some of these cells (n = 14) were within multiple-use MPAs and so did not contribute to the achievement of objectives requiring coverage by no-take areas. In contrast, without the requirement for existing MPAs to be part of the solution, the objectives were met with 9% of reef cells (Fig. 5.9C). In this analysis, few reef cells appeared to be substantially more important than others (only 11 of the 428 reef cells had a selection frequency of 100%, Fig. 5.9D). These 11 reef cells were mostly located in the central sector and included the two reef cells within regime 1.

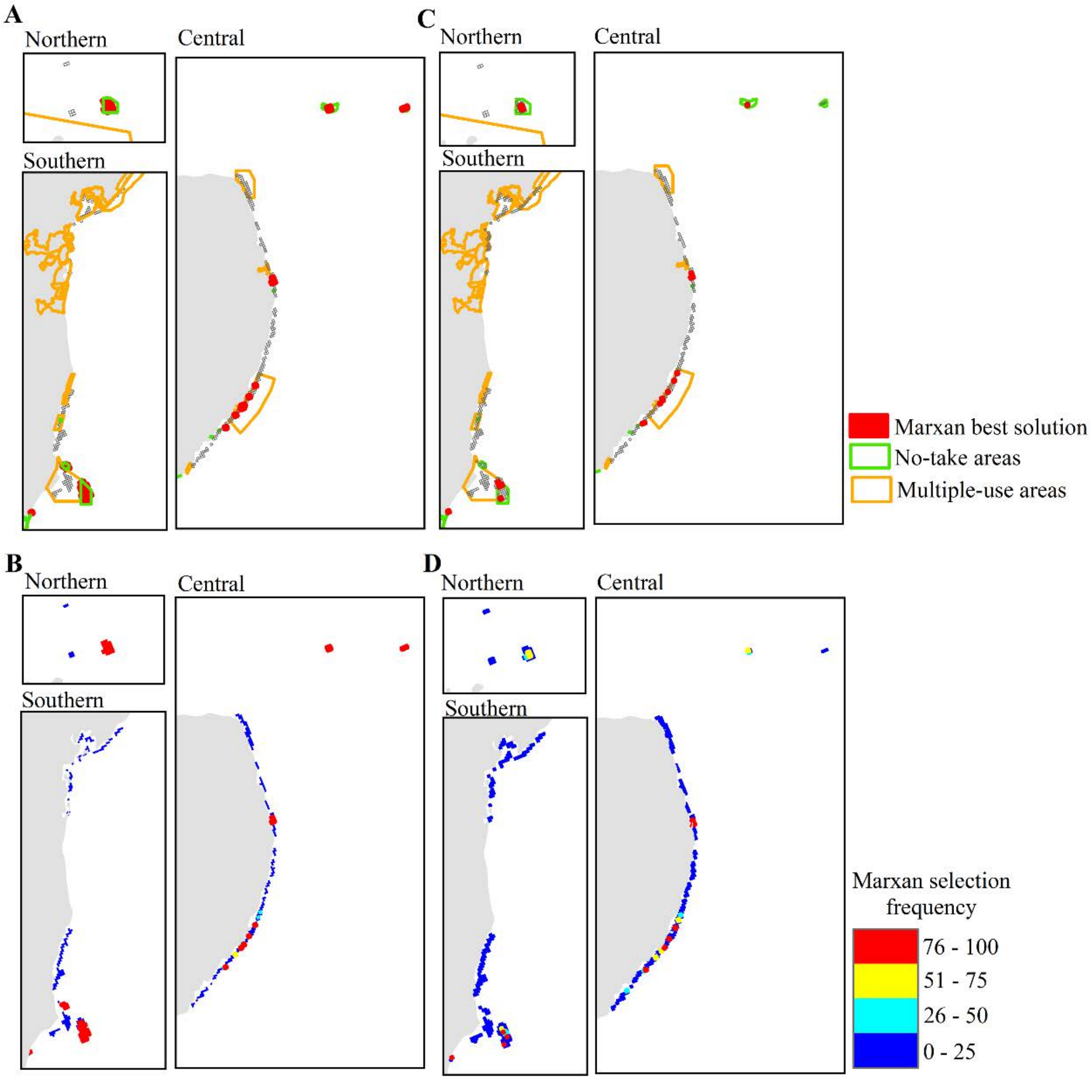


Figure 5.9 Spatial prioritization of coral reefs in Brazil based on the conservation objectives for incorporating warming disturbances. Maps show best solution and selection frequency Marxan outputs when selection of reef cells coinciding with existing MPAs was mandatory (A and B, respectively) or optional (C and D, respectively). Views for reefs in the northern, central, and southern sectors of the study area correspond to insets in Fig. 5.2A.

5.4 Discussion

Mitigation and avoidance of warming disturbances are challenging issues for MPA planning. Designing effective MPA systems will require explicit management objectives and approaches that account for shifts in climate disturbances over time. Using chronic and acute thermal-stress metrics based on observed and projected SST data, I explored ways of assessing the adequacy of an MPA system under current and future climate circumstances when MPA boundaries were not spatially or temporally flexible. I showed that the waters of all coral reefs in Brazil have warmed and will continue warming. Events of acute temperature stress, and associated bleaching and potentially mortality, are expected to increase in frequency and intensity on the majority of the reefs studied. After setting explicit management objectives for reef cells in different temperature regimes, I demonstrated that the existing MPA system has important shortfalls, including unmet conservation objectives for historical and/or future thermal refugia. Some of the under-represented reef cells are spatially very restricted along Brazil‘s central coast.

5.4.1 Retrospective time-series

I found that Brazilian coral reefs were warming faster than the global average of 0.17 ± 0.05 °C decade^{-1} (Good et al. 2007), but less quickly than the averages for the Caribbean province of 0.29 °C decade^{-1} (Chollett et al. 2012) and the Coral Triangle of 0.2 °C decade^{-1} (Peñaflor et al. 2009). Thus, the Western Atlantic coast might provide more favorable environmental conditions than other coral-reef regions for adaptation of the most thermally-sensitive species during global warming. Although climate change might be occurring more quickly than the rate at which most species can effectively respond through local adaptation or migration across seascapes (Hoegh-Guldberg 1999; Hughes et al. 2003; Makino et al. 2014b), an urgently-needed extension of this and previous studies is a systematic comparison between coral-reef provinces, identifying areas globally where changes in climate are consistently attenuated. Secure protection of areas with low chronic stress might provide many opportunities for species persistence.

While recent instances of coral bleaching in the study area have been correlated with warming sea temperatures (Krug et al. 2013), there have also been mismatches between the timing of bleaching phenomena in some of my reef cells and major global events related to the periodic occurrence of ENSO variability (Baker et al. 2008; Berkelmans et al. 2004; Krug et al. 2013; Leão et al. 2008). Because bleaching events in Brazil (as elsewhere) are also driven by interactions with other stressors, such as eutrophication and sedimentation, a more comprehensive evaluation is needed for assessing exposure to other key factors that reinforce or reduce thermal stress (see Maina et al. (2011)). Although considering different types of interactions between local and global stressors is important for management (Brown et al. 2013), assessing their combined disturbance is rarely straightforward. It can be technically demanding, requiring collection of datasets for environmental factors other than temperature, as well as better understanding of ecological consequences of interactions. While my work is focused on warming disturbances, it provides management insights that are beneficial to advance reef conservation and decision-making by pinpointing areas where fine-resolution information on local stressors is particularly important.

The observed patterns of bleaching-level stress indicate that my study area has been exposed to DHW levels similar those of other areas across the globe (Donner et al. 2007; McClanahan et al. 2007a; McClanahan et al. 2007b). Temporal mismatches between bleaching events observed in some of my reef cells and those in other reef provinces exposed to similar levels of acute thermal stress might also be explained by the lack of systematic effort in the reporting of bleaching in the western Atlantic Ocean. Bleaching data are essential for a better understanding of patterns of bleaching disturbance in response to thermal stress (McLeod et al. 2012) and could be used to validate bleaching thresholds such as mine with information that is species- or site-specific. The available evidence indicates that not all corals respond identically to thermal stress; sensitivities vary substantially across species (Hughes et al. 2003). Background SST variability can also influence the thermal sensitivity of coral communities (McClanahan et al. 2007b).

5.4.2 Prospective time series

PCM1 predictions of warming disturbances in the period 2010–2099 demonstrate that, although the rate of warming is less than in recent decades, an incremental increase in the frequency and severity of bleaching-level events associated with massive mortality is expected for the majority of reefs in the southern sector. While such models provide an initial assessment of future vulnerability to thermal stress, PCM1 is among the models with lowest sensitivity; for example, for a doubling of CO_2, the projected temperature increase is only 1.5 ºC (van Hooidonk et al. 2015). Consequently, my results for bleaching-level events are likely to be underestimated. Importantly, the spatial distribution of metrics derived from projected time series did not coincide with those based on the historical dataset. Therefore, my findings indicate that MPA designations that ignore predictions for thermal stress might have little ability to adequately capture future distributions of thermal-stress regimes.

While I attempted to minimize the influence of other sources of variability in the future climate by selecting only one emission scenario, Makino et al. (2014a) have argued that priority should be given to areas that are selected consistently across all available scenarios as a way to identify no-regrets sites for conservation. From this point of view, one way forward is to establish robustness of results by examining the extent to which different scenarios of greenhouse-gas emissions would affect the spatial delineation of thermal regimes. By doing so, it might be possible to find a consensus among climate forecasts and shed light on the upper and lower bounds of uncertainty related to climate projections that will help to predict future conditions more accurately.

Although assembling a set of GCMs could offer a more comprehensive analysis of SST projections, I opted to use only one model output because different GCMs vary in their ability to correctly capture some aspects of SST, such as the amplitude of the seasonal cycle and variability due to El Nino-Southern Oscillation (ENSO) (Meehl et al. 2007; van Hooidonk and Huber 2012; Wu et al. 2008). It is important to note that the assembly of multi-model predictions is very data-intensive and beyond the scope of this study, which aimed primarily to illustrate the potential benefits of incorporating modelled projections into conservation objectives.

Despite the employment of only one scenario and model output, my work demonstrates one ecologically meaningful way of interpreting and combining warming projections with reserve design. Although including projected changes in climate into MPA design carries inherent uncertainties (Heller and Zavaleta 2009), there is an urgent need to integrate proactive approaches within conservation plans to better understand future states and reduce the risk of poor conservation outcomes (Moss et al. 2010; Strange et al. 2011; van Hooidonk et al. 2015). While I acknowledge assumptions in the ecological components of my modelling, model-based uncertainties can be reduced by the adoption of an adaptive planning framework for conservation (Pressey et al. 2013). The potential refinements to my current procedures would increase their ecological relevance and enhance the functional capability of areal classification by thermal-stress regime. The refinements can also be readily accommodated within my framework as more refined information becomes available.

5.4.3 Conservation objectives for dealing with warming disturbances

Conservation is unlikely to be successful or efficient in the long term if shifts in climate disturbances are not considered. My results show that, although the current MPA system incorporates some of my warming-disturbance regimes, other important areas need protection through consideration of current and future thermal-stress regimes. While there is increasing pressure for evaluation of protected areas with respect to their intended objectives (Wilson et al. 2009), MPA systems designed to represent static features might fail to meet objectives for spatially- and temporally-dynamic phenomena (Ban et al. 2012; Hobday 2011); it is therefore necessary to incorporate dynamic phenomena into the process of objective setting. Prioritization through the formulation of quantitative and well-defined objectives in combination with a spatially- and temporally-explicit methodology for planning with ecologically-informed parameters provides a best approach to planning for dynamic threats (Magris et al. 2014).

Calls to address climate-related disturbance by increasing MPA size or replicating features of interest in widely-spaced MPAs are widespread (Magris et al. 2014). These guidelines reflect the difficulty of understanding of ecosystem responses to environmental change and to formulate quantitative objectives accordingly. Also, implementation of these general and usually qualitative recommendations might be impractical in real-world situations where there are severe spatial constraints on the extent of MPAs. Furthermore, MPA expansion is difficult to justify without well-argued objectives. I have improved upon more general recommended strategies for addressing climate change by proposing a methodological template to address specific warming-related variables to develop conservation objectives underpinned by ecological information. This study also demonstrated the value of combining retrospective information that might be valuable over the short term as a bet-hedging strategy (see Chollett et al. (2014)) with projected SST to delineating thermal-stress regimes. As borne out by my analysis, current patterns of SST anomalies might not necessarily be indicative of the future (Ban et al. 2012; McLeod et al. 2012; Selig et al. 2012).

In addition to using both historical and projected SST to better respond to warming disturbances in marine planning, my conceptualization of objectives offers at least two other improvements on previous approaches. First, it acknowledges that many management types are needed for planning in the context of climate change (Anthony et al. 2014; Baker et al. 2008; McClanahan et al. 2012). With information on current and future exposure to warming disturbances, managers will be more able to identify areas requiring local actions for controlling non-climatic threats and will allow a broader temporal perspective when assessing the required level of active management and the most suitable MPA category under conditions of climate warming.

Second, my spatial prioritization was also framed such that severity of warming disturbances triggered long-term conservation objectives. All previous studies have taken one of three approaches in the definition of timeframes: (i) calculating geometric means for predictions at arbitrary temporal intervals (Game et al. 2008b); (ii) using midpoints or endpoints in the time series for fixed assessments as benchmarks (Carroll et al. 2010; Hobday 2011; Makino et al. 2014a; Makino et al. 2014b); or (iii) including a large number of time steps in a data-intensive approach (Levy and Ban 2013). While I accounted for the whole time series for predicting shifts in disturbance regimes to estimate long term degradation rate, I also addressed the situation of temporally-static MPAs being preferable due to ease of implementation. Since there might be legislative, political, or implementation challenges in the creation of dynamic MPAs (Day 2002; Game et al. 2009; Hobday 2011), my proactive MPA design provides an option for planners to address future states with static MPA boundaries. Although there are several limitations related to spatially fixed reserves (see Alagador et al. (2014)), dynamic conservation planning involving selection of new MPAs and removal of others must be viewed with caution if this will risk undermining the integrity of the remaining MPA system by weakening protection to facilitate extractive uses.

SST data and projections provide only one layer of information when informing decisions about MPA placement. Including spatially-explicit data on socioeconomic variables (Ban and Klein 2009) species occurrences (Rondinini et al. 2006), and dynamic factors relating to connectivity (Magris et al. 2015b) will broaden my methods and determine whether the spatial patterns of conservation that emerge from my methods would be changed by other considerations. Importantly, I did not account for other threats to determine where multiple stressors occur concurrently, which could lead to incorrect identification of sites requiring management. The combined effects of multiple stressors need to be further assessed, particularly because the disturbances of climate warming are compounded by those arising from local human activities, over which managers have direct influence (van Hooidonk et al. 2015).

It might also be possible to incorporate other significant disturbances of climate change on coral reefs, such as ocean acidification and sea-level rise (see McLeod et al. (2012)), into MPA design to fully understand how future ocean conditions can be accommodated by conservation planning. Incorporating only metrics of thermal stress means that my framework should be regarded as a first step for conservation planners to deal with climate-change disturbances.

My classification of regimes offers insights into coral-reef conservation, although I believe that this approach can be adapted to inform conservation of other marine ecosystems. For example, studies in rocky reefs, kelps, seagrasses, and mangroves have also identified climate-warming effects on ecosystem functioning (Comeaux et al. 2012; Jordà et al. 2012; Russell et al. 2009; Wernberg et al. 2011). Such effects could be interpreted for conservation planning into a similar framework to mine, as could regimes integrating information across other disturbances related to climate change.

5.5 Conclusions

My aim was to help decision-makers in prioritizing areas considering long-term vulnerabilities to climate warming. I developed an approach to MPA design with a spatially- and temporally- quantitative procedure that accounts for historical and projected sea surface temperature. I projected, on the basis of GCM modelling, that bleaching-level stress in Brazil will tend to increase while the rate of warming appears to decrease, and interpreted these changes relative to recovery times of coral communities. I also determined the extent to which existing Brazilian MPAs achieve the conservation objectives in the face of dynamic threats and showed how additional MPAs might be designed to account for both historical and future thermal stress. Using a prospective approach such as mine is advantageous when anticipating shifts in predicted disturbance regimes in cases where temporally-static MPAs are more feasible than dynamic ones that can be shifted to accommodate future conditions.

Chapter 6. Integration of biodiversity, connectivity and climate warming in marine planning reveals the value of setting multiple conservation objectives[5]

Abstract

Decision makers focus on representing biodiversity, maintaining connectivity, and strengthening resilience to climate change when designing MPA networks. However, the development of MPAs intended to achieve these goals might fail if multiple conservation objectives are not adequately formulated from the outset of marine planning. By using Brazilian coral reefs as a case study, I devised conservation objectives regarding biodiversity, connectivity and climate warming and determined the extent to which MPAs achieve them. In doing so, I explored interactions between different sets of objectives and evaluated the consequences of pursuing single objectives in marine planning. I found that MPAs in Brazil are more effective for biodiversity than for connectivity and climate warming. Moreover, I identified that a high level of misfit between existing MPAs and priority areas that strategically achieve a well balanced set of objectives was widespread. Although better synergies were found when planning directly for biodiversity, multiple objective approaches would provide best opportunities to greatly benefit MPA design. Notably, I showed that conversion of multiple-use areas into no-take MPAs is the greatest requirement to fill conservation gaps. Also, this requirement would not incur a substantial additional cost in the management expenses in comparison to designing of an entirely

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[5] This chapter is yet to be submitted as ―Magris R.A., Pressey R.L., Floeter, S., Vila-Nova, D., Mills, M. Journal to be decided".

new network of MPAs. My analysis reinforce the utility, feasibility, and value of setting multiple conservation objectives and provides timely support for efforts to expand MPAs in Brazil, and yield insights for MPA planners elsewhere.

6.1 Introduction

With rapidly increasing rates of habitat deterioration and climate warming, the design and implementation of MPAs represents an important tool for fostering conservation, providing insurance and recovery following disturbance and mitigating climate-related impacts (Di Minin and Toivonen 2015; Gaines et al. 2010; McLeod et al. 2009). However, while several studies have documented the effectiveness of existing MPAs at providing conservation benefits and restoring ecosystem components (e.g. Almany et al. (2013); Berumen et al. (2012); Harrison et al. (2012)), many aspects related to their design criteria (e.g. location, size, spacing) continue to be driven by opportunity or political interests (Devillers et al. 2015). The opportunistic placement of MPAs might undermine their long-term effectiveness and, hence, make the entire system –residual”. Thus, systematic conservation planning, based on objective-driven prioritisation, is fundamental to help create MPAs that are able to attain clearly stated goals and obtain maximised benefits to biodiversity persistence with limited funds.

Quantitative conservation objectives are the foundation for systematic conservation planning (Margules and Pressey 2000), and are central towards understanding resource-allocation consequences and the acceptability of any prioritisation problem (Game et al. 2013). The formulation of such objectives can accommodate representation of biodiversity patterns, in addition to ecological and threatening processes related to the long-term maintenance of biodiversity, such as larval connectivity and climate change within an overarching framework (Pressey et al. 2007). Despite these processes being increasingly incorporated into decision making strategies in recent years (Magris et al. 2014), most marine planning exercises typically develop objectives that represent static elements of biodiversity (e.g. Giakoumi et al. (2011); Green et al. (2009)). Therefore, an important step in conservation planning methods is setting objectives for processes that enhance the ability of MPAs to guarantee the persistence of conservation features through time. For example, representation objectives for biodiversity are probably insufficient to guarantee species persistence if an MPA system is composed of widely spaced separate MPAs, because the maintenance of viable populations is disrupted through a lack of connectivity. Similarly, conservation objectives that do not account for projected climate change might decrease the likelihood of biological diversity coping with rapid climate warming.

To date, several studies have proposed advanced approaches towards designing well-connected MPA systems (e.g. Beger et al. (2010b); Jacobi and Jonsson (2011); White et al. (2014)) and towards helping enhance ecosystem functioning in times of climate warming (e.g. Chollett et al. (2014); Game et al. (2008b); Makino et al. (2014a). However, the interactions between the objectives for connectivity and climate change have yet to be explored in detail. Furthermore, these studies have overlooked potential synergies between process-related objectives and objectives related to patterns of biological diversity.

The integration of multiple objectives in marine planning might result in unrealistic and politically challenging conservation plans, due to a demand for larger areas for conservation. Thus, network of MPAs should be developed to span a spectrum of protection levels that help minimise these challenges. Marine spatial planning that incorporates multiple MPA types (hereafter referred to as ―MPA zones") provides planners and policy-makers with more flexibility to accommodate the objectives that satisfy the demand for multiple considerations, compared with a traditional two zone planning process (i.e. reserve zones versus non-reserve zones) (Crowder et al. 2006). Spatial prioritization that considers different conservation zones has been typically used to generate plans with more equitable socioeconomic impacts (e.g. Klein et al. (2009); Makino et al. (2013); Weeks et al. (2010b)). Yet, to date, published studies have not accounted for variability in the management schemes in which MPAs are embedded as an attempt to accommodate multiple objectives.

Here, I apply a planning tool with zoning to overcome the lack of integration of multiple objectives in conservation plans, and to generate insights that contribute towards achieving a suite of strategic conservation goals (i.e. biodiversity, connectivity, and climate warming) in a complementary manner. First, I aimed to ascertain the degree to which the MPA system intended to protect Brazilian coral reefs (as an example) fulfils a multiple set of objectives. Second, I tested whether the current level of conservation effectiveness (i.e. objective achievement) would be different in MPAs that were strictly designed to achieve these strategic objectives were set up. Third, I examined the potential gain received from multiple objectives in a hypothetical MPA network typically designed to account for single objectives. Fourth, I evaluated the ability of existing MPAs to conform to a plan that accommodates multiple, concurrent objectives. I anticipated that well balanced conservation plans might be formulated by developing a prioritization method that combines multiple conservation objectives from the outset of MPA planning.

6.2 Material and Methods

6.2.1 Study area

My analysis focused on Brazilian coral reefs, which are among the highest conservation priority areas in the Atlantic Ocean due to their high endemism levels and the presence of structures that are significantly different from those in most other parts of the world (Leão et al. 2003). Brazilian coral reefs cover a linear distance equivalent to nearly 2,500 km of coastline, occurring mostly in the eastern and northeastern Brazilian continental margin, with sparse occurrence in the north. These reefs are clearly under stress due to human activities (Pinheiro et al. 2010; Segal and Castro 2011), and the current MPA system is biased in relation to spatial coverage and restriction levels, which can make ongoing conservation efforts ineffective (Magris et al. 2013).

6.2.2 Conservation planning definitions

Conservation prioritization involved assembling input data for biodiversity, connectivity, and climate warming; the development of the respective conservation objectives; compilation of MPA data; and the use of conservation planning tool to simulate scenarios. For terminology I used in the present study, see Table 6.1.

Table 6.1 Terminology developed for my conservation planning study.

Definitions	
Conservation feature	Each species, ecosystem type, or functional group that represent the biodiversity of the study area or any process-related measure associated with connectivity or climate-related variables that have a conservation interest
Conservation objective	Quantitative requirement (i.e. a numeric target) of a minimum amount of each feature that needs to be conserved through an MPA network
Set of objectives	A group of conservation objectives for features within a certain strategic conservation goal (i.e. biodiversity, connectivity, or climate change)
Reef cells	Square grid cells containing coral reef that could be potentially selected for protection by conservation planning tool (i.e. planning units)
MPA zones	A certain type of MPA based on their management intent and intended level of protection (i.e. no-take or multiple-use areas)
Scenarios	Application of conservation planning tool to resolve conservation objectives, which must ensure achievement of a set of objectives, individually or altogether, and produce amenable solutions to management

6.2.3 Conservation features

Biodiversity

Using the best and most current publicly available information on Brazilian reefs, I defined ecosystem types and reef-fish species distribution as surrogates for biodiversity, encompassing a total of 174 conservation features, which were summarised within each reef cell. I used spatial data representing coral reef ecosystems derived from satellite imagery (high and very high spatial resolution) and developed a hierarchical classification scheme that would accomplish a finer delineation of this ecosystem than in my former study (Magris et al. 2013). I combined the extension of coral reef ecosystems devised from visual interpretation of georeferenced imagery with the boundaries of ecoregions, geomorphologic types, bathymetry data, and tidal zone discrimination to assign coral reefs into 23 distinct and non-overlapping classes of ecosystem types (see Appendix C6). I assumed that this classification into broad physiographically uniform classes of ecosystem types was likely to capture main aspects regarding biodiversity patterns over a large geographic gradient.

I obtained species distribution data for 405 species of reef fish from a geographic range data set compiled by Vila-Nova et al. (2014). Reef fish species play important roles in coral reef ecosystems through regulation of food webs and nutrient cycling (Mouillot et al. 2014), and represent the most studied marine group with robust distribution data along the Brazilian coast (Vila-Nova et al. 2014). For each species, I obtained information on biological traits relevant to their habitat requirements and ecological vulnerability (Halpern and Floeter 2008), including: body size (maximum body length), maximum depth, and trophic category. These traits can be used to describe the fish functional niche and its relative impact in essential coral reef ecosystem services (Mouillot et al. 2014) and to render populations with enhanced susceptibility to stressors (Bender et al. 2013). Based on this analysis, I mapped range distribution for each of the 79 functional fish groups developed through all combination of biological traits, for which objectives were derived.

To account for those species that have the greatest conservation need I used the national Red List of Threatened Species (Brasil, 2014), to classify the reef-fish species into three levels according to their extinction risk, for which I formulated conservation objectives: (i) Vulnerable (VU), (ii) Endangered (EN), and (iii) Critically Endangered (CR). Altogether, 32 species were listed under the extinction risk levels and had their distribution maps extracted from Vila-Nova et al. (2014). Additionally, acknowledging the prominent role of geographic range size in determining the risk of extinction (Harnik et al. 2012), I also listed endemic species according to Vila-Nova et al. (2014) and assigned a conservation objective for each species‘ range distribution; endemic species numbered 47.

Connectivity

I used spatial data about demographically significant dispersal links between reef cells representing connectivity (Magris et al. 2015b). Connectivity is defined as the likelihood that, for a particular modelled species, larvae originating at a source coral reef are capable of reaching neighbouring reef cells. Ecological connectivity was modelled for four different species, that represented different life history traits, to capture a range in species dispersal potential (a brooder coral, a broadcast spawning coral, a roving herbivorous fish, and a large carnivorous fish) and resulting asymmetric connectivity-probability matrices were used to produce metrics (i.e. out-flux, betweenness centrality, and local retention) associated with each species. Further details on the parameterization of larval simulations can be found in Magris et al. (2015b).

Based on the findings from my previous work (Magris et al. 2015b), I further stratified the connectivity metrics for two coral reef species across three subregions within my study area (i.e. northeastern, central and southern coast) to define conservation features related to connectivity. By doing so, I attempted to capture feature occurrences across a range of subregions that reflect major breaks in the connectedness for those species. This ensures sufficient replication of important reefs in the face of the reduced dispersal ability of short-distance dispersers. By combining three connectivity metrics for four model species and the three subregions (considered for only two coral reef species), I ended up with 24 conservation features, each with an explicit conservation objective.

Climate warming

My climate warming conservation features were derived from spatial delineation of thermal stress regimes undergone by Magris et al. (2015a). By using measures of chronic and acute thermal stress and combining historical and projected data sets, nine thermal stress regimes occurred across the study area and warranted conservation attention as a way to tackle protection against climate-related disturbances. Those regimes corresponded to six types of thermal refugia (i.e. regimes containing varying levels of historically and/or future stable conditions but with limited bleaching stress level) and three types of disturbance-related areas (i.e. regimes subjected to climate-related disturbances and thus more likely to contain thermally tolerant species).

All the regimes should be factored into an analysis of conservation priorities specifically because they affect the mechanisms associated with avoidance of climate disturbances, mitigation of cumulative stresses, ability to individuals to adaptively respond to thermal stress, and future resistance to warming (Magris et al. 2015a). Further details of how each metric was calculated and how the metrics were combined to delineate thermal regimes are given in Magris et al. (2015a).

6.2.4 MPA data

I compiled data on existing MPAs along the Brazilian coast, including their legal boundaries (Magris et al. 2013). This study focused on an MPA system containing two zones: (i) no-take areas, which are set aside to protect biodiversity and allow only non-extractive uses of natural resources, such as for educational and scientific activities (IUCN categories I to IV); and (ii) multiple-use areas, which have the objective of promoting the sustainable use of the marine environment by a wide variety of groups and permit, but regulate, various extractive activities (IUCN categories V and VI). A total of 18 MPAs were identified along Brazilian coast spatially coinciding with coral reef ecosystems. The existing no-take MPAs cover nearly 55% of the coral reef area, whereas coverage by multiple-use MPAs is about 35% (Magris et al. 2013).

6.2.5 Conservation objectives

Rather than using uniform percentages as objectives, I refined my conservation objectives to account for the diverse management requirements and vulnerability of each feature. The conservation objectives encompassed two components: one overall objective, aiming to be met by any MPA zone; and a zone-specific objective, based on an objective associated to a certain type of zone. Conservation objectives were developed based on initial hypotheses of the amount and level of protection necessary to sustain our conservation features over time.

Biodiversity

Representation objectives for ecosystem types and functional groups ranged from 10-30% of their distribution, depending on the spatial extension of each ecosystem within the study area and combination of biological traits within each functional group. For ecosystem types, I set area-based objectives by linear interpolation, in which the maximum objective coverage corresponds to those ecosystems with smaller spatial extension and the minimum objective for those with greater spatial extension. For functional diversity, I scaled the objectives in such a way that larger objectives were associated with biological traits that reflect increased vulnerability and with greater likelihood of population declines. For instance, functional groups comprised by large-bodied and corallivore fish species associated with shallow habitats are disproportionally more affected by reef degradation than others (Bellwood et al. 2004; Genner et al. 2010; Mouillot et al. 2014), and thus received more demanding objectives. By summing up the contribution of each trait within each functional group, I had objectives ranging from 11.3% to 28.7%.

For threatened and endemic species, I stipulated that the objectives be inversely scaled with the species geographic range size and directly incremented according to their conservation status following recent approaches (Guilhaumon et al. 2015; Venter et al. 2014). The representation objective for endemic and non-threatened species was equal to 50% of the geographic range for those with a restricted distribution and to 10% for widespread species, and it is interpolated log-linearly for all the other species in between. Representation objectives were then increased for threatened species, and further incremented for species both endemic and threatened (n = 7). Although I also defined those objectives by interpolating a linear function of the log-transformed range size for threatened species, I further applied a rule for minimum protection coverage following the conservation status of each species. Critically endangered species had representation objective of 100% irrespective of their range size.

A baseline zone-specific objective was set as one third of the overall objective within no-take zones for each ecosystem type, functional group, and for those non-endemic and threatened species. I then allowed this percentage to vary following the conservation status of species and the level of endemism. The most demanding zone-specific objective was assigned to critically endangered species with restricted range (100% of the overall objective within no-take zones). Further details about objective assignment for all types of biological features are provided in the Appendix C6.

Connectivity

I defined my connectivity objectives according to the percentage of values represented by the subset of reef cells containing the top third values for each metric (Magris et al., 2015b). Objectives then varied from 50 to 90% of their normalised values across conservation features (see Appendix C6 for details). Because the connectivity metrics are related to replenishment of larvae, increased potential recovery, and capacity to be self-sustaining and given uncertainties surrounding effectiveness of multiple-use areas, I applied my conservation objectives only for no-take zones (i.e. all objectives were then zone-specific).

Climate warming

Conservation objectives were set according to the needs and specific management requirements explained in Magris et al. (2015a). In this approach, zone-specific objectives were defined considering historical or future ecosystem state of each regime (e.g., areas facing a low level of historical thermal stress are potentially unmodified areas that could still retain a naturally functioning ecosystem and be suitable as no-take zones). Furthermore, the percentage objectives were defined according to previous studies stating the importance of protecting sites under specific thermal stress regimes. Based on a gradient of ecological relevance, the objectives were set as 100, 50, or 30% of coverage within a specific zone (see Magris et al. (2015a) for details).

6.2.6 Gap analysis

To evaluate the effectiveness with which MPAs achieve different sets of objectives, I carried out a gap analysis to assess how well the existing spatial arrangement of MPAs accomplishes the overall biodiversity, connectivity, and climate warming conservation objectives. To investigate the number of features that missed their conservation objective and the amount by which the objective was missed, I calculated the percentage of spatial overlap between reef cells in which the conservation features occur in the study area and the percentage of spatial overlap between those reef cells and MPAs of each zone. I then compared this overlap with the original objectives for each feature and quantified the overall biodiversity, connectivity, and climate warming representativeness (Obj_a) by averaging the feature objective achievement:

$$Obj_a = \sum_{1\ldots N}^{i} \frac{\left(\frac{Pi}{Obi}\right)*100}{N} \qquad (6.1)$$

where Pi is the proportion of conservation objective Obi accomplished for the feature i , and N is the total number of conservation features.

6.2.7 Conservation scenarios

I considered three conservation scenarios to explore interactions between sets of objectives: (i) no further MPA implementation (i.e. leaving the current level of objective achievement as identified by my gap analysis); (ii) an expanded MPA scenario, which complements the current protection by fully achieving each set of objectives individually and all simultaneously; and (iii) a clean slate scenario, which identifies a notional network of MPAs that would also optimally achieve alternative set of objectives without acknowledging the current protection. To generate both the expanded and clean slate scenarios, I used the Marxan with Zones conservation planning software (Watts et al. 2009), which allowed me to include both the overall and zone-specific objectives. To provide consistency across scenarios, I resampled all conservation features into reef cells 10 x 10 km (the coarser spatial resolution for our spatial data) for use in Marxan with Zones (see Appendix C6).

For the expanded scenario, I ran Marxan with Zones to identify the most efficient set of reef cells that, if protected, would fulfill the objectives left unmet by existing MPAs while minimizing costs. For the clean slate scenario, Marxan with Zones could freely select reef cells for protection, regardless of their current protection status. I defined a coastal development index (Rowlands et al. 2012) as a cost, which indicates a current presence of human infrastructure and was used as a proxy measure of the degree of impediments to conservation management. To differentiate the cost for a given reef cell to be allocated as either a no-take or a multiple-use zones, I extracted budget information from published management costs of existing MPAs in Brazil. On average, I found that no-take zones were 2.3 times more costly than multiple-use ones, and used this number as a multiplier for the cost measures. Details about the calculation of the cost are given in the Appendix C6.

In the expanded scenario, I also evaluated the additional coral reef protection required within each zone to achieve each set of objectives (as a percentage of the total coral reef area). For this calculation, I measured coral reef area in reef cells identified by Marxans' best solution (i.e selected reef cells that meet the conservation objectives at the lowest cost). Given that existing MPAs constrains the total coral reef area available for further protection when fully achieving all objectives, I allowed existing multiple-use zones to be upgraded to no-take areas. For this analysis, I had another Marxan with Zones run considering only existing no-take zones as mandatory part of Marxan's best solution (i.e. locking them in). The coral reef area within reef cells identified by the best solution that overlapped with existing multiple-use zones were used to compute the coral reed area requiring strength in the protection. Further details about Marxan with Zones parameters for all scenarios are describe in the Appendix C6.

6.2.8 Comparison between scenarios

I evaluated the consequences of the implementation of the notional network of MPAs identified in the scenarios above by: (1) assessing total annual management cost and (2) analysing of incidental objective achievement.

The total annual management cost of implementing network of MPAs was calculated as a function of the coral reef area required to be protected for each combination of scenario and set of objective. In doing so, I could predict the additional management costs required to expand the existing MPAs and consider potential cost saving had a systematic approach to MPA planning been implemented historically. Management costs associated with implementing MPAs in Brazil were predicted using a linear model by which the total cost incurred in protection is budgeted in accordance with existing management plans, and accounting for the size of the proposed network of MPAs within each type of zone. MPA size is a major driver associated with financial resources for conservation (Gravestock et al. 2008). Further details about my management cost models are described in the Appendix C6.

To illustrate the implications of planning for different objectives, I examined the impact of pursuing biodiversity, connectivity, and climate warming objectives individually on the achievement of other objectives. The incidental objective achievement was assessed based on the benefit attained for the non-targeted objectives as a result of additional protection related to the targeted objective. The objective achievement proportions were assessed by using Eq. 6.1, as described in the gap analysis section. For the purpose of this analysis, I performed ANOVA to evaluate differences in the achievement of objectives between both expanded and clean slate scenarios in relation to the existing MPAs for each set of objectives.

6.2.9 Adequacy of the existing MPA to achieve multiple objectives

I reported the selection frequency outputs from Marxan with Zones (i.e. how often each reef cell is selected for an indicated zone) that satisfied all conservation objectives for the clean slate scenario as a way to better assess the adequacy of existing MPA systems in achieving multiple objectives. Areas were classified as high, medium, or low priority by using natural breaks in the selection frequency outputs for each zone. I sought to summarize areas identified as having the highest level of importance for achieving multiple objectives, but which remain unprotected, and areas with the lowest importance but which are currently covered by MPAs. I then analysed the adequacy of the current protection level by intersecting the priority area scores for each zone with the MPA boundaries as an attempt to easily visualize where a high or medium level of misfit is present and where a suited fit exists.

All data manipulations and analyses described above were implemented within the R statistical programming environment (R 3.1.3; R Core Team, 2015). Geospatial manipulations were performed within ArcGIS 10 environment.

6.3 Results

Objective achievement varied significantly between the three sets of objectives (Fig. 6.1): MPAs on average achieved 88% (median equal to 100%) of the objectives for biodiversity features, performing poorly for climate warming and connectivity features (means drop to 44 and 12.8%, respectively). I found that about 58% of biodiversity features (i.e. 105 features) met both their overall and zone-specific objectives. Conversely, 12 conservation features had 0% achievement for both overall and zone-specific objectives. The level of representativeness for coverage by no-take zones was lower than that calculated for the whole system. Specifically, nearly 40% of the biodiversity features had 0% achievement in their zone-specific objectives related to no-take, while only 9% of the features reached this value when considering the overall objectives. Separating the results by the type of biodiversity feature (see additional results in the Appendix C6), threatened species had the best representativeness among the other three types of biodiversity features (i.e. ecosystem types, functional diversity and endemic species), despite having much more demanding objectives. While supporting a better level of objective achievement for biodiversity, the protection coverage given to biodiversity features within each type always ranged from 0% to 100%.

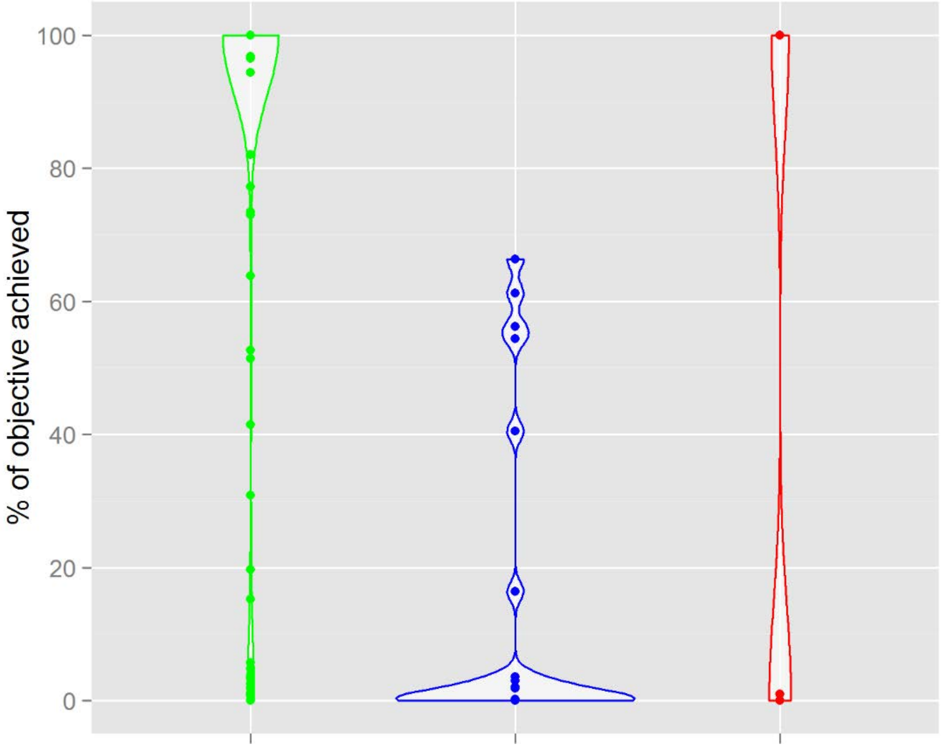


Figure 6.1 Percentage of objective achievement for biodiversity (green), connectivity (blue), and climate warming (red) by existing MPA system in Brazil. Dots represent each conservation feature within each set of objectives. Violin graphs show the the density of features with a certain level of objective achievement (as an illustration of frequency distribution). Results stratified within each set of objectives are shown in the Appendix C6.

Connectivity was marked by a high relative concentration of features (i.e. 18 features), with a low level of achievement (less than 10%) and a 65% maximum percentage of objective accomplishment being recorded (for the combination snapper and out-flux). Betweenness centrality received the lowest level of protection out of all three metrics, with about 2.5% of their values were located within MPAs. The objectives of 12 conservation features were completely missed by the existing MPA system. The distribution of values for objective achievement was highly skewed for climate warming (objective achievement around either 0% or 100%). Out of all thermal refugia types, only one type (historical thermal refugia projected to face increased stress in the future) fell within existing MPAs. All of the remaining thermal refugia were located outside MPAs or were covered by MPAs other than no-take. Thermally-disturbed regimes largely occurred within established MPAs (mostly no-take), with their objectives being fully achieved.

To achieve the objectives fully for all conservation features, several types of spatial adjustments were required for the expanded scenario, with additional coral reef area requiring protection (Fig. 6.2). For instance, connectivity mostly required that a large amount of coral reef area currently protected by multiple-use areas is converted into no-take zones (about 20% out of the 35% already covered by multiple-use zones). Among the three sets of objectives, climate warming demanded the largest amount of additional new no-take and multiple-use zones (5.5% from the total coral reef area). As the majority of objectives had already been achieved, requirements for biodiversity objectives primarily included upgrading 5% of coral reefs protected by established multiple-use zones to no-take zones. When all of the objectives were combined, we estimated that about 95% of the total coral reef area would need to be protected by some type of MPA zone. The greatest requirement is the conversion of parts of the multiple-use zones to no-take areas, and was primarily driven by connectivity objectives.

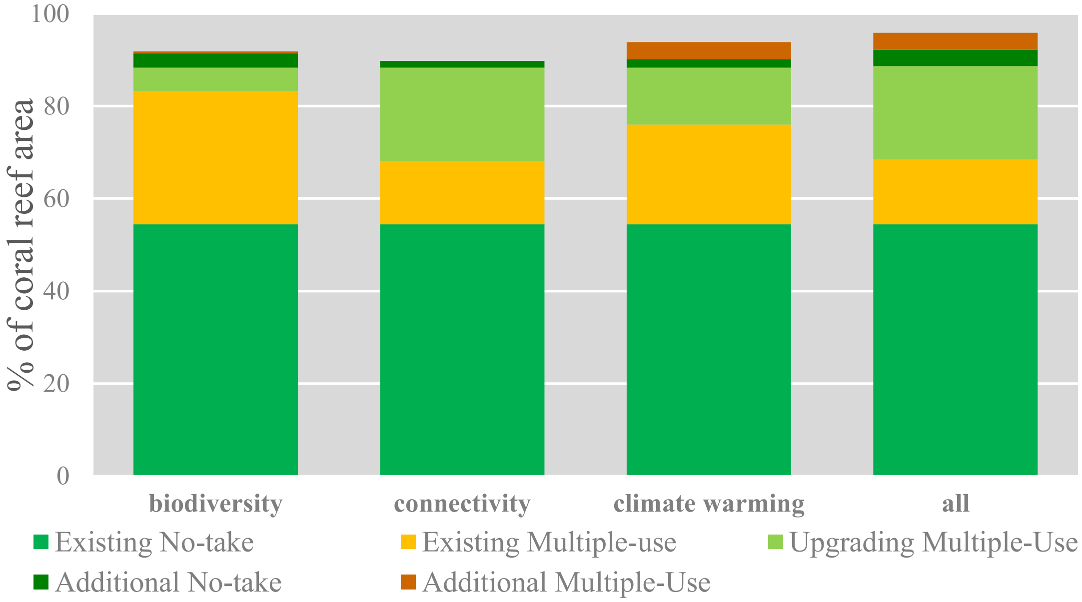


Figure 6.2 Spatial adjustments required when expanding the existing MPA system to fully achieve each set of objectives and all objectives combined. Assessments were made in terms of coral reef area and are shown separately for each set of objectives and all combined. The expanded scenario shows the portion of coral reef that remains within existing no-take and multiple-use MPAs, the additional coral reef coverage required to be allocated within new no-take and multiple-use areas, and the area of existing multiple-use areas required to be upgraded to no-take MPAs.

Management costs to maintain the existing MPA system protecting coral reefs were estimated to be around 3.9 million US $ per year (Table 2). The requirements to increase the amount of coral reef area covered by MPAs in the expanded scenario were reflected in a slight increment of the total management costs for all sets of objectives (greatest increase for climate warming, i.e. approximately 0.17 million US $ per year to protect an extra 20 km^2). Although the clean slate scenario would save a large amount of expenses to achieve connectivity and climate change objectives separately (roughly 0.7 and 2.7 million US $ per year, respectively), planning for biodiversity objectives would make the costs of a clean slate scenario comparable to the costs of the expanded scenario. Consequently, an increase in the estimated management costs would still be necessary (i.e. 0.47 million US $ per year) when planning for all objectives together, if I disregarded the existing system (i.e. clean slate scenario) in relation to the estimated cost for existing MPAs. Furthermore, I estimated that the clean slate scenario would reduce management costs by only 0.3 million US $ per year in comparison to the expanded scenario when planning for multiple objectives (all conservation features included).

Table 6.2 Costs incurred when implementing MPAs according to different sets of objectives and scenarios. Estimations are provided in US $ annual cost and are based on regression analysis model described in the Appendix C6.

Scenario	Sets of conservation objective			
	Biodiversity	Connectivity	Climate warming	All
No further MPA implementation (existing MPAs)	3,929,139.00			
Expanded MPAs	4,079,730.30	4,095,443.10	4,107,572.80	4,697,914.90
Clean slate MPAs	4,299,897.80	3,221,511.40	1,178,042.20	4,399,553.60

I investigated whether planning for one of each set of objectives would yield a reasonable achievement outcome for non-targeted objectives in the planning (incidental objective achievement, see Fig. 6.3). When expanding the existing MPA system, I found that planning for biodiversity resulted in the best overall conservation benefit, as it would achieve a significantly higher proportion of the connectivity and climate warming objectives in relation to the existing level of achievement ($p < 0.05$). Conversely, planning for climate warming would cause the worst marginal conservation benefit, with no significant increase detected for biodiversity and connectivity objectives with respect to the current level of achievement ($p > 0.05$).

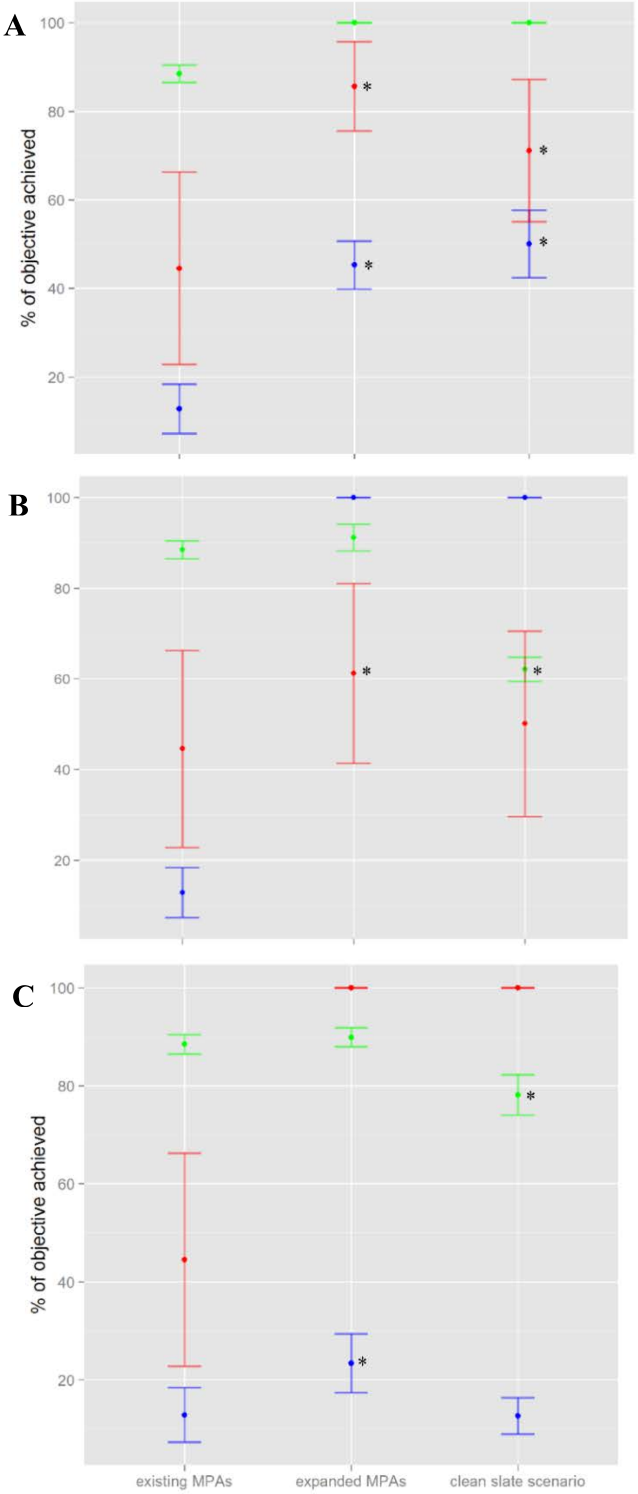
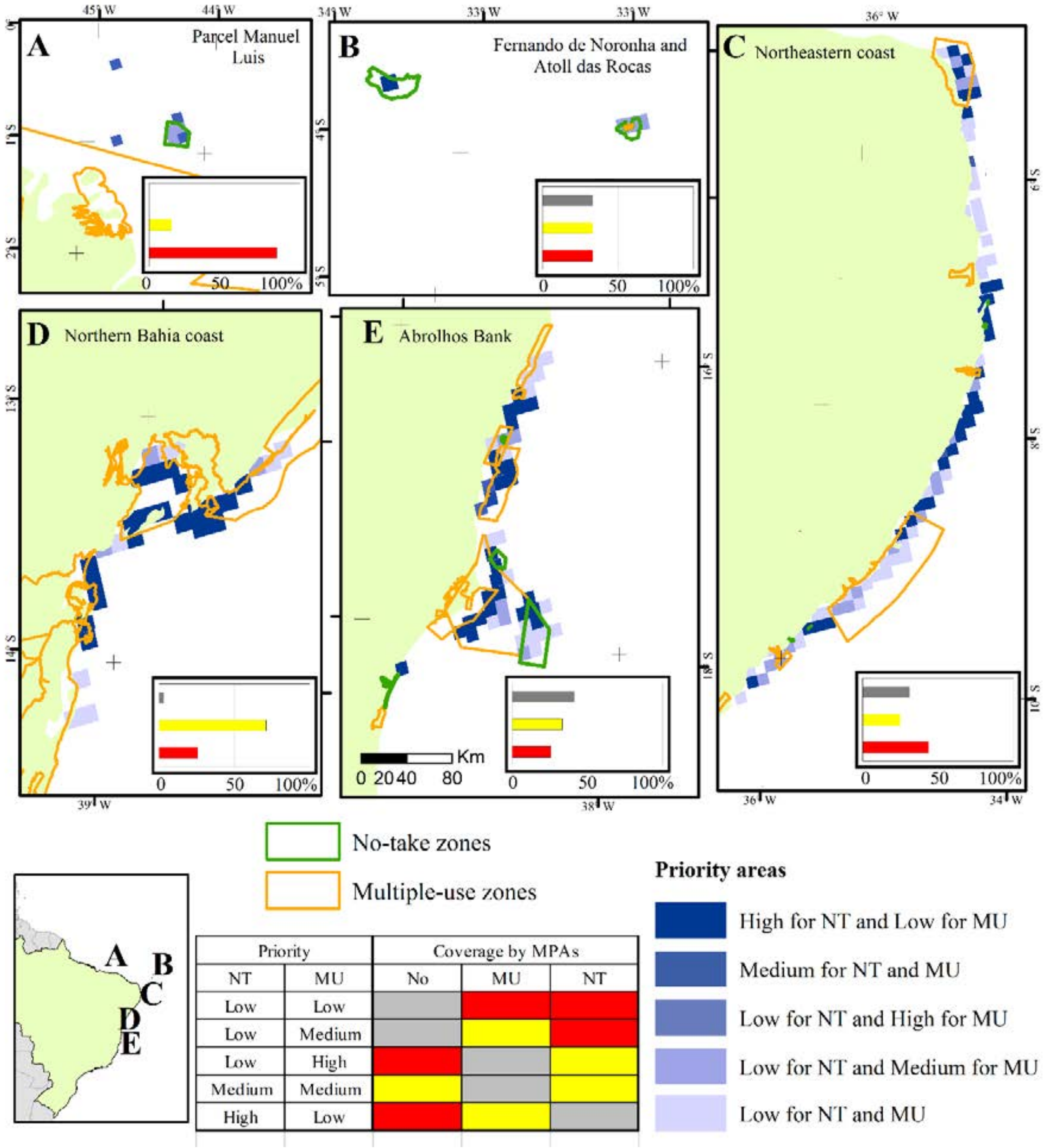


Figure 6.3 The incidental achievement of conservation objectives when planning for biodiversity (a), connectivity (b), and climate warming (c). Mean objective achievements (and standard error) are

*represented for three conservation scenarios: no further MPA implementation (existing MPAs); expanded MPA network; clean slate scenario.*P<0.05 for ANOVA comparisons against existing MPAs.*

When evaluating whether a clean slate scenario would perform better than expanding the existing one, I found that implementing a hypothetical new MPA system would not be more successful than expanding the current system. This is because targeting any set of objectives yielded significantly lower levels of achievement for other sets of objectives (e.g. lower level of achievement of climate change objectives when planning for biodiversity) or reached no significant difference in relation to the expanded scenario (e.g. statistically similar level of achievement for climate change objectives when planning for connectivity).

When assessing the adequacy of the existing MPAs in relation to an ideal MPA system fully achieving multiple objectives, I observed that a very high level of misfit was widespread (43% of coral reef cells). Of concern, only 22% of the reef cells had an appropriate fit (Fig. 6.5). However, noticeable regional differences were detected in the extent to which priority areas were included in the correct management category, with reefs in the southern areas showing a reduction in the high level of misfit (i.e. Abrolhos Bank, see Fig. 6.5E). In contrast, reefs located in the very north of our study area (i.e. Parcel Manuel Luis, see Fig. 6.5A) had the highest misfit (reaching 75% of the reef cells present in this sector).



Priority		Coverage by MPAs		
NT	MU	No	MU	NT
Low	Low	▨	🟥	🟥
Low	Medium	▨	🟨	🟥
Low	High	🟥	▨	🟨
Medium	Medium	🟨	▨	🟨
High	Low	🟥	🟨	▨

Figure 6.4 Adequacy of the existing MPA system when planning for multiple objectives. The rank of priorities reflects the selection frequency of reef cells when all objectives were included. 176 reef cells were grouped into five sectors (A-E) to facilitate geographic visualisation. Inset graphs show the misfit analysis based on the intersection between priority areas and the current system of MPAs (depicted as a percentage of the total reef cells within each sector): red represents very high level of misfit (e.g. high priority area outside any type of MPA); yellow for a medium level of misfit (e.g. medium priority areas within no-take MPAs); and grey illustrates where there is an appropriate fit (e.g. low priority areas outside any type of MPAs).

6.4 Discussion

My analysis indicates that diverse synergies are produced when planning directly for biodiversity, connectivity and climate warming; however, my approach also highlights the consequences that arise when any one of the objectives is overlooked. For instance, a plan targeting areas that retain high biological diversity might generate a series of areas conferring a moderate degree of resilience to climate change, which only marginally contribute to the maintenance of important dispersal pathways. Thus, I propose that the integration of these three goals in the initial stage of planning would avert an unbalanced achievement of objectives. My findings also indicate that, despite large spatial extension of MPAs protecting Brazilian coral reefs, the existing MPA system is more effective for biodiversity than for connectivity and climate warming.

In certain circumstances, major significant synergies emerged between particular objectives (e.g. planning for biodiversity achieves a large portion of climate warming objectives). However, the greatest benefit for ecological relevance would be gained if multiple objectives were accounted for in conservation plans. There is a significant information gap regarding the appropriate objectives for process-related features, particularly with respect to connectivity and climate warming, in the marine conservation literature (Magris et al. 2014). However, recent research has provided examples reaffirming that a comprehensive view of ecological considerations is required to enhance effective decision-making. For instance, Mumby et al. (2011) found that including thermal stratification and connectivity into reserve design had a significant impact on network configuration and performance. Similarly, White et al. (2014) recommended that adding connectivity information to representation prioritisation increases reserve network performance. My results reinforce these preceding publications, by demonstrating that the extent of spatial overlap between sets of objectives is variable and might limit the total conservation benefit when focusing on separate objectives.

For all conservation objectives to be adequately addressed, the expansion of existing MPAs would require an increase of 0.7 US $ million in annual management costs. Proposed MPA size is a consistently good predictor of management cost per unit of area (Ban et al. 2011). Furthermore, here, I show that considerable benefit to MPA conservation accomplishment could be achieved with modest additional costs. However, my cost analyses should be treated with caution. First, I considered relative cost based on management cost only, not opportunity costs for other marine uses. Expanding protected areas requires managing trade-offs among societal objectives (Polasky et al. 2008); thus, cost predictions should include impacts on other activities. Second, my predictions were made based on management plans for existing MPAs that encompassed a range of marine environments, not just coral reefs. Thus, I had to assume that type of ecosystem being protected did not interfere in management cost predictions. Finally, my statistical linear model did not capture any polynomial relationship between per-unit-area management cost and MPA size (Ban et al. 2011).

Resolving the trade-offs between social and conservation goals is challenging in the context of conservation planning for multiple objectives. Additional objectives lead to larger required total areas of MPAs, and implementation of very extensive MPA systems might be economically unfeasible and politically unrealistic. Driven by the desire to balance conservation objectives and stakeholders interests, an MPA zoning process has commonly been used by planners to manage human demands and conservation with reduced conflicts (Grantham et al. 2013; Makino et al. 2013; Metcalfe et al. 2015). My research could be extended to assess these inherent trade-offs in a spatial zoning context as socioeconomic information is gathered, and to ensure that priority areas identified are as cost-effective as possible.

I also found that, while the national MPA system in Brazil provides sufficient protection for a large number of biodiversity features related to coral reefs, these MPAs significantly failed at meeting the objectives for climate warming and connectivity features. This issue might arise because Brazilian MPAs were primarily implemented to cover areas of high biological value (Amaral and Jablonski 2005), which might lead to the biased protection found across conservation features. In addition, our objectives for connectivity and climate warming were all zone-specific, which makes these objectives harder to attain because they need coverage by a specific type of zone in the MPA. Although a small number of reef cells (22%) were adequately covered by MPAs, considerable progress towards protecting coral reefs has been made. For Brazil to meet the Aichi target (CBD 2013), multiple priority setting objectives must be reconciled to increase the likelihood that biodiversity patterns persist, and to deliver a more equitable distribution of conservation effort among features.

My study extends the scope of my previous gap analysis (Magris et al. 2013) by refining generic quantitative objectives for coral reefs. Consequently, I show that high levels of biological representation might not be informative about the effective level of protection, particularly when taking a more complementary view to traditional gap analysis. I stress the importance of incorporating functional diversity for MPA networks to be representative of all biodiversity components, in addition to biogeography, evolutionary, and phylogenetic diversity, as suggested by Guilhaumon et al. (2015). Moreover, even areas that are currently classified as MPAs might be ineffective for many other reasons, such as a lack of resources or poor management agency coordination (e.g. Gerhardinger et al. (2011)), impairing the existing level of effectiveness. The relative contribution of MPAs towards realising conservation objectives is unlikely to be always correlated to the extent of protection, due to their falling under different management categories (Mills et al. 2011). Therefore, other biological features in need of protection must be identified, taking variable management effectiveness of different MPA zones into account. As a result, my inferences can change, allowing other conservation gaps to emerge.

Planners often pursue individual objectives for the sake of simplicity or better communication with stakeholders (Wilson et al. 2009). However, the explicit recognition of synergies between different conservation goals would ease conservation effort, help align strategies, and optimise the allocation of limited management resources, ultimately supporting improved decision-making processes. Studies in the last five years have focused on investigating how to continue expanding MPAs without impairing socio-political factors at local (Adams et al. 2011; Game et al. 2011; Hamel et al. 2012; Vilar et al. 2015), and global (Halpern et al. 2010) scales. However, explicit consideration of gains between conservation objectives might help identify opportunities for win-win strategies that contribute to meeting multiple objectives with limited financial resources. While Green et al. (2014a) recently proposed guidelines for the achievement of multiple objectives, quantifying the co-benefits of planning for multiple objectives has not been considered. Furthermore, the capacity of biodiversity conservation to represent other ecosystem services (surrogacy capacity) has also been questioned in the terrestrial realm (Chan et al. 2006). Yet, the surrogacy effect between protecting biodiversity and the maintenance of ecological processes related to connectivity and climate threats mitigation requires addressing. Thus, I emphasise the need for more strategic thinking when setting and implementing MPAs to maximise synergies in conservation effort, in addition to evaluating the existing level of conservation effectiveness.

I recognise that MPA expansion is one of several tools that might be used to realise conservation goals. Considering the whole suite of conservation tools available to achieve conservation (i.e. fishing restrictions, catchment-based management) would likely result in more complex interactions towards achieving the different objectives. Thus, further investigations of the synergies and trade-offs of these complex interactions are required. Moreover, the interactions among objectives might change over time, given the temporal dimension of MPA effectiveness when evaluated against multiple objectives. For example, Andrello et al. (2015b) showed that the effect of climate on connectivity would reduce the ability of MPAs to provide benefits to exploited areas in the future. Additional objectives must be delineated to identify all potential significant interactions of climate change (as well as vulnerability to other expanding threats) on connectivity and biodiversity, to tailor more informed conservation plans.

Chapter 7. General discussion

The ultimate goal of marine conservation planning is to design efficient MPAs that ensure long-term benefits for biodiversity and sustainable use of resources (Bottrill and Pressey 2012; Halpern et al. 2010; Wood et al. 2008). This is often realised through the use of decision-support tools that identify priority areas for conservation. Hence, a growing body of research seeks ways to include measures of persistence into spatial prioritisation (Game et al. 2008b; Moffitt et al. 2011a; White et al. 2014). However, the procedures whereby conservation features related to persistence can be incorporated into MPA design have not yet been developed comprehensively. Missing from these efforts is the formulation of conservation objectives that take a more holistic perspective on the integration of processes related to species‘ persistence into MPA placement. My thesis contributes to filling this gap by seeking to advance conservation planning for persistence, and addressing the question of how MPA planners are able to develop an informed decision-making process.

I propose methodological frameworks for improving marine planning for persistence, using coral-reef ecosystems as an example. Globally, the spatial coverage of MPAs to protect coral reefs is particularly high (Mora et al. 2006), and the rate of MPA expansion for coral reefs is greater than for any other ecosystem or taxonomic group (Butchart et al. 2015). Because MPAs are the most commonly applied form of spatial management for fostering coral-reef conservation, I argue that conservation outcomes provided by MPAs could be enhanced through a framework that formally integrates key processes supporting coral-reef biodiversity over the long term. This framework is imperative: contemporary conservation planning needs to assess the effectiveness of past management decisions in light of new insights, as well as to build these insights into future conservation scenarios.

7.1 Towards a strategic integration of connectivity and climate warming in marine conservation

Calls to address the integration of ecological and threatening processes related to the long-term maintenance of biodiversity within MPA design, such as larval connectivity and climate warming, are widespread (Almany et al. 2009; Fox et al. 2011; Green et al. 2014b; McCook et al. 2009; McLeod et al. 2012; McLeod et al. 2009). Accordingly, coral ecologists are increasingly focused on measuring the importance of connectivity in conservation (Martin et al. 2015; Olds et al. 2014; Pittman et al. 2014) or vulnerability of coral populations and species to climate-induced disturbances (McClanahan et al. 2007b; Mumby and Harborne 2010; Osborne et al. 2011). The most compelling challenge is, however, the integration of emerging concepts and modelling techniques to shed light on the appropriate formulation of conservation objectives.

In this thesis, I have proposed an overarching framework (Chapter 3) to develop conservation objectives that would enable planners to improve evidence-based decision-making, and deliver better conservation strategies. By describing a sequence of six approaches to more effectively integrate connectivity and climate warming into conservation plans, I demonstrated how MPA planners could move towards addressing persistence at the beginning of the conservation planning process. Conservation planners often have trouble explicitly framing conservation objectives (Game et al. 2013), a difficulty that can undermine the utility of objectives in practical applications (Pressey and Bottrill 2009). This requires defining conservation objectives more clearly, so my work was an attempt to make their formulation operationally meaningful and generally applicable for more effective conservation.

7.2 Formulation of persistence-related conservation objectives for marine planning

My review of the literature identified that recommendations for integrating connectivity and climate warming into marine planning through conservation objectives presently have important shortcomings. These limitations include the limited use of empirical evidence to inform decisions and the infrequent identification of quantitative requirements for conservation (Chapter 3). Because of this lack of practical and evidence-based applications, my thesis postulates that stronger methodological frameworks will better operationalise the integration of connectivity and climate warming into marine conservation planning.

In this context, I have developed novel methodological frameworks to support conservation planning, primarily favouring the development of well-connected (Chapter 4) and climate-resilient (Chapter 5) networks of MPAs. Previous work has attempted to incorporate connectivity (Beger et al. 2010b; Edwards et al. 2010; Lehtomäki and Moilanen 2013; White et al. 2014) and climate warming (Game et al. 2008b; Levy and Ban 2013; Mumby et al. 2011) into MPA design. However, my thesis tackles important conceptual, theoretical, and methodological difficulties that have not previously been addressed.

When planning for connectivity, key advances provided by my study included: (i) the development of ecologically informed connectivity objectives; (ii) the inclusion of threatening processes in the calculation of connectivity metrics that were reflected in spatial priorities; (iii) the incorporation of multiple species encompassing a variety of life-history traits into planning for connectivity; and (iv) the investigation of the extent to which the combined connectivity matrix acts as a proxy for species with different dispersal abilities.

When planning for climate warming, key improvements upon previous approaches were: (i) setting explicit conservation objectives for reefs in different temperature regimes that require a range of management options (MPA types); (ii) combining retrospective with prospective time-series information on sea-surface temperature to delineate thermal-stress regimes; and (iii) demonstrating a spatial prioritization that is framed by long-term conservation objectives for situations in which temporally-static MPAs are more feasible than dynamic ones due to ease of implementation.

7.3 The value of setting multiple conservation objectives to promote biodiversity persistence

Conservation outcomes will be enhanced if planning considers all biotic variation across the planning region, the full range of ecological effects that are modulated by connectivity and climate-warming processes, and the spatial and temporal scales over which these processes operate. Typically, MPA design aims to represent a targeted amount of key habitats assumed to be sufficient to achieve persistence-related objectives (Giakoumi et al. 2011; Klein et al. 2008a). My results demonstrated that management efforts are more likely to be effective if a more comprehensive view is taken from the initial stages of conservation planning (Chapter 6). My results also draw a key conclusion that spatial coverage of MPAs (Chapter 2) can be a poor indicator of conservation effectiveness (i.e. objective achievement). When a much more sophisticated gap analysis was undertaken than the one described in Chapter 2, I found (in Chapter 6) that most of the existing MPAs that are aimed to protect coral reefs are actually placed in sub-optimal locations; they are unable to accumulate larvae, to function as migratory pathways, or to increase resilience against warming disturbances.

In Chapter 6, I integrated, for the first time, pattern-based conservation features (i.e. ecosystems and species distributions) with ecological processes related to connectivity and climate warming disturbances, aiming to attain the goal of ensuring conservation of biodiversity for future benefit. This also represents the first study to evaluate potential synergies in marine conservation between process-related objectives and objectives related to patterns of biological diversity at an ecologically relevant scale. While practices of systematic conservation planning towards marine ecosystems are in their infancy in Brazil (Chapter 2), the spatial prioritisation presented here might help support existing commitments to maintain biodiversity, and future efforts for expanding the existing MPA system.

7.4 Future research directions

Some of the research directions for better understanding of marine conservation planning are indicated by the main limitations of the work presented in this thesis and the caveats on interpretation of my results. Specifically, these main limitations and caveats are:

- The need to explore the nature of tradeoffs involved when important areas for conservation compete for space with extractive uses, and choices are needed about which objectives should be met and which will not be achieved;
- Better understanding of the primary drivers of ecosystem health, their influence on connectivity patterns, and their relationship with resilience to warming disturbances;
- Lack of information on MPA effectiveness that could be considered to further fine-tune frameworks for planning, increasing the realism in future applications of planning for persistence.

Although my analyses demonstrate the derivation and application of conservation objectives regarding connectivity and climate warming, future research should also track ways to capture the full range of complexities related to biodiversity conservation. This is an ongoing task, with continuing methodological and data improvements, which enhance our understanding of connectivity and climate-warming effects on coral reefs. While the current methodological frameworks address some limitations, some general challenges remain.

For example, it remains to be seen whether consideration of social and economic contexts and dynamics prevents the conservation objectives regarding biodiversity, connectivity, and climate warming to be simultaneously achieved. Importantly, we also need to understand the extent to which these objectives could be numerically compromised and how the tradeoffs might be resolved when not all sets of objectives can be fully achieved.

Another promising avenue for future research is to investigate dependencies between, on one hand, the proxies that are meant to characterise climate-related variables or connectivity features of interest and, on the other hand, empirical data on ecosystem functioning, which would help to inform proxies and objectives and quantify real conservation outcomes. Empirical data on direct measures of coral-reef state (i.e. coral cover, species composition, species abundance) and on bleaching disturbances would refine and enhance the capacity of modelling approaches to predict functional consequences for population dynamics and guide the development of a more transparent methodological framework. This integration of modelling and empirical perspectives provides the basis for fully understanding the mechanisms that influence ecosystem viability and resilience, and increases the underpinning ecological knowledge upon which management guidelines are devised.

Studying the effects of climate warming on connectivity patterns will shed light on the formulation of temporally-explicit connectivity objectives and is important for understanding ecological responses of organisms as warming progresses during this century. At present, little is known about how features of the seascape (i.e. species abundance and their connectivity patterns) will respond to increased frequency and the magnitude of warming disturbances. The key future direction is the development of a dynamic approach to predicting how connectivity can directly help to reduce the degradation trend of coral reefs, given the temporal variation in all vulnerability components (i.e. exposure, sensitivity, and adaptive capacity) of coral-reef ecosystems with ongoing climate change.

My gap analyses highlight the utility of incorporating variability in the ecological effectiveness of MPAs into conservation planning. It is well understood that the success of MPA networks in terms of threat mitigation and ecological benefits requires consideration of their effectiveness, such as aspects of management and enforcement. While quantifying the extent of MPAs is important, there is a lack of measurement of their real-world effectiveness and evaluation of whether it varies across different MPA types. Therefore, an important next step that must be emphasised is a careful evaluation of the management effectiveness of Brazilian MPAs to yield further insights on how well conservation objectives are actually fulfilled.

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Appendices

Appendix C1 - Other papers in preparation during my candidature

Magris R.A., Andrello M., Stephanie M., Mouillot D., Dallongeville A., Pressey R.L. The value of connectivity and representation information in conservation planning: design a reserve network to achieve persistence.

Magris R.A., Grech A., Pressey R.L. Cumulative impacts of human activities on coral reefs in Brazil.

Mills M., Bonaldo R.M., Kerber I.K.G., Lima M.C.S., **Magris R.A.**, Fuentes M.M.P.B., et al. Ways forward for marine spatial planning in Brazil.

Appendix C2 – Additional Methods and Results for Chapter 2

Habitat map

Habitat and marine resource management maps were compiled, using ArcGIS v10 software. The habitat maps were derived from three sources: a subtidal benthic map, built using high-resolution bathymetry data (Becker *et al*. 2009), and maps of coral reef habitat (Brasil 2006) and mangrove ecosystems (Magris & Barreto 2011). Depth zones, mangrove, coral reef habitat and ecoregions were used to define benthic habitats. Further subdivision of habitats was constrained by lack of data on marine biodiversity. Distributional data of all marine species have not yet been mapped with spatial consistency, so I had to assume that mangroves, coral reefs, depth categories and ecoregions reflect physical attributes relevant to species composition. For the same reasons, habitat surrogates have been used extensively for marine biodiversity assessments and conservation prioritizations, and are regarded by many as suitable alternatives to direct data on species (Klein *et al.* 2008; Mills *et al*. 2011).

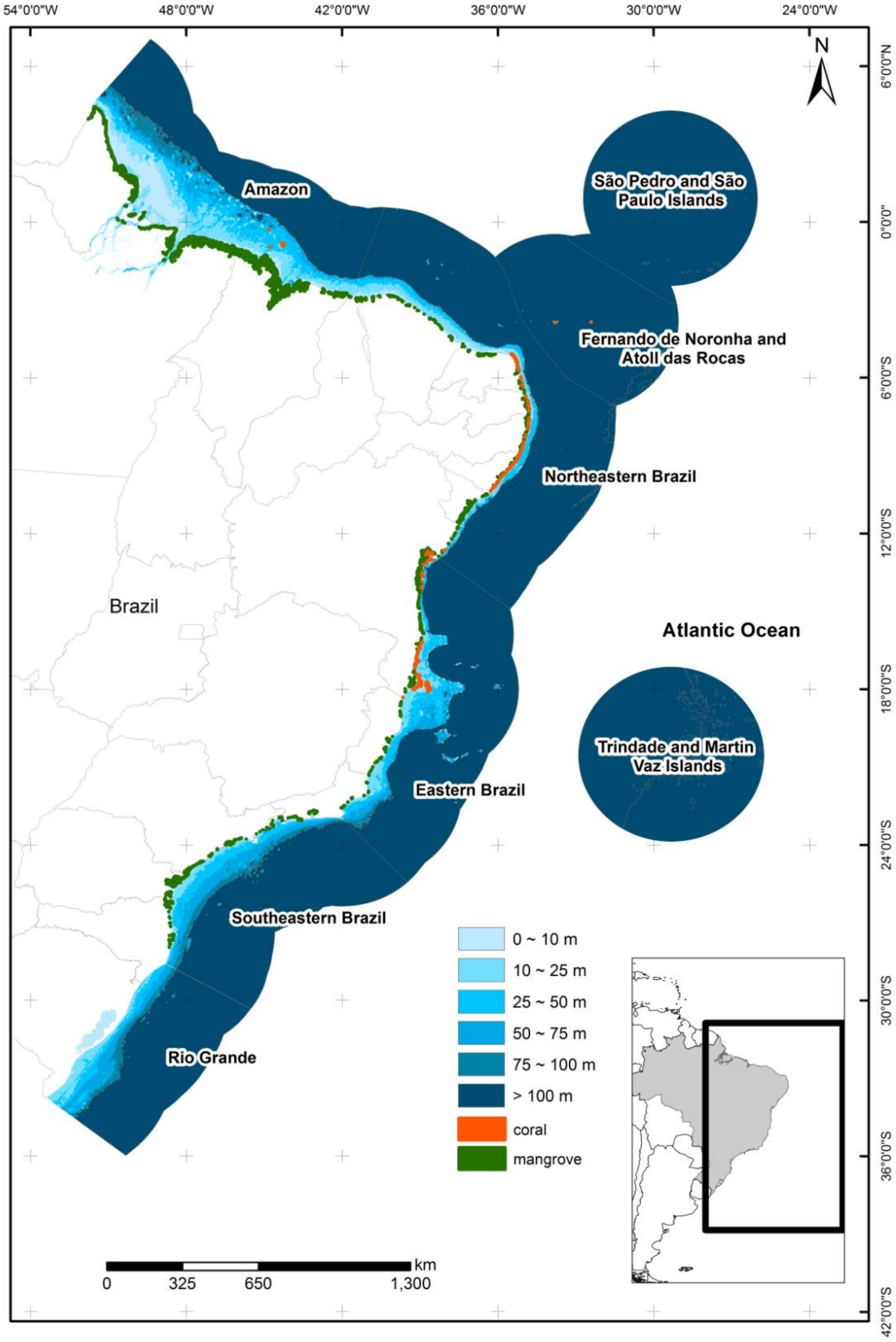
Six depth zones were extracted from an interpolation procedure, in which I rescaled a 1 km-resolution satellite-gravity model to produce a spatial depth model at 500 m resolution. Bathymetry, coral reef and mangrove data were intersected with the boundaries of marine ecoregions that span the southwestern Atlantic region (Spalding *et al*. 2007). I combined my eight ―primary” habitats (coral reef, mangrove, and other substrata in six depth zones: 0-10m, 10-25m, 25-50m, 50-75m, 75-100m, and >100m) with eight ecoregions: 1. Amazon; 2. Northeastern; 3. Eastern; 4. Fernando de Noronha and Atoll das Rocas; 5. São Pedro and São Paulo Islands; 6. Trindade and Martin Vaz Islands; 7. Southeastern Brazil; and 8. Rio Grande. This intersection produced 56 habitats (less than 64 because not all combinations were present).

Management map

Three categories were used to group areas that provided similar levels of protection to biodiversity: 1. no-take areas, set aside to protect biodiversity and allowing only non-extractive uses of natural resources such as educational and scientific activities; 2. extractive reserves, where biodiversity conservation is combined with sustainable use of natural resources by traditional communities; and 3.

multiple-use areas, with objectives to promote the sustainable use of the marine environment by a wide variety of groups. Extractive reserves are established in conjunction with traditional groups to protect livelihoods and cultures and the natural resources on which they depend. Multiple-use areas encompass large areas in which various extractive activities are permitted but are regulated, spatially and temporally, to a greater extent than areas outside these MPAs.

The MPA classification corresponds to those management categories under the National System of Conservation Units (SNUC) Law in Brazil and the International Union for Conservation of Nature and Natural Resources (IUCN) category system relating to various levels of protection. I refer to no-take areas as those termed ―Ecological Station”, ―Biological Reserve”, ―National Park”, ―Natural Monument”, and ―Wildlife Refuge” by SNUC. These correspond to IUCN categories I, II, III, and IV. I refer to extractive reserves as those named ―Extractive Reserves” and ―Sustainable Development Reserves” by SNUC. These correspond to IUCN category V. I refer to multiple-use areas as those labelled ―Environmental Protection Areas”, and ―Areas of Relevant Ecological Interest” by SNUC. These correspond to IUCN category VI.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30°0'0"S
36°0'0"S
42°0'0"S
N
Amazon
São Pedro and São Paulo Islands
Fernando de Noronha and Atoll das Rocas
Northeastern Brazil
Brazil
Atlantic Ocean
Trindade and Martin Vaz Islands
Eastern Brazil
Southeastern Brazil
Rio Grande
0 ~ 10 m
10 ~ 25 m
25 ~ 50 m
50 ~ 75 m
75 ~ 100 m
> 100 m
coral
mangrove
km
0
325
650
1,300

Figure C2.1 The 56 marine habitats considered in my analysis, embracing mangrove, coral reef, other benthic substrata, and ecoregions.

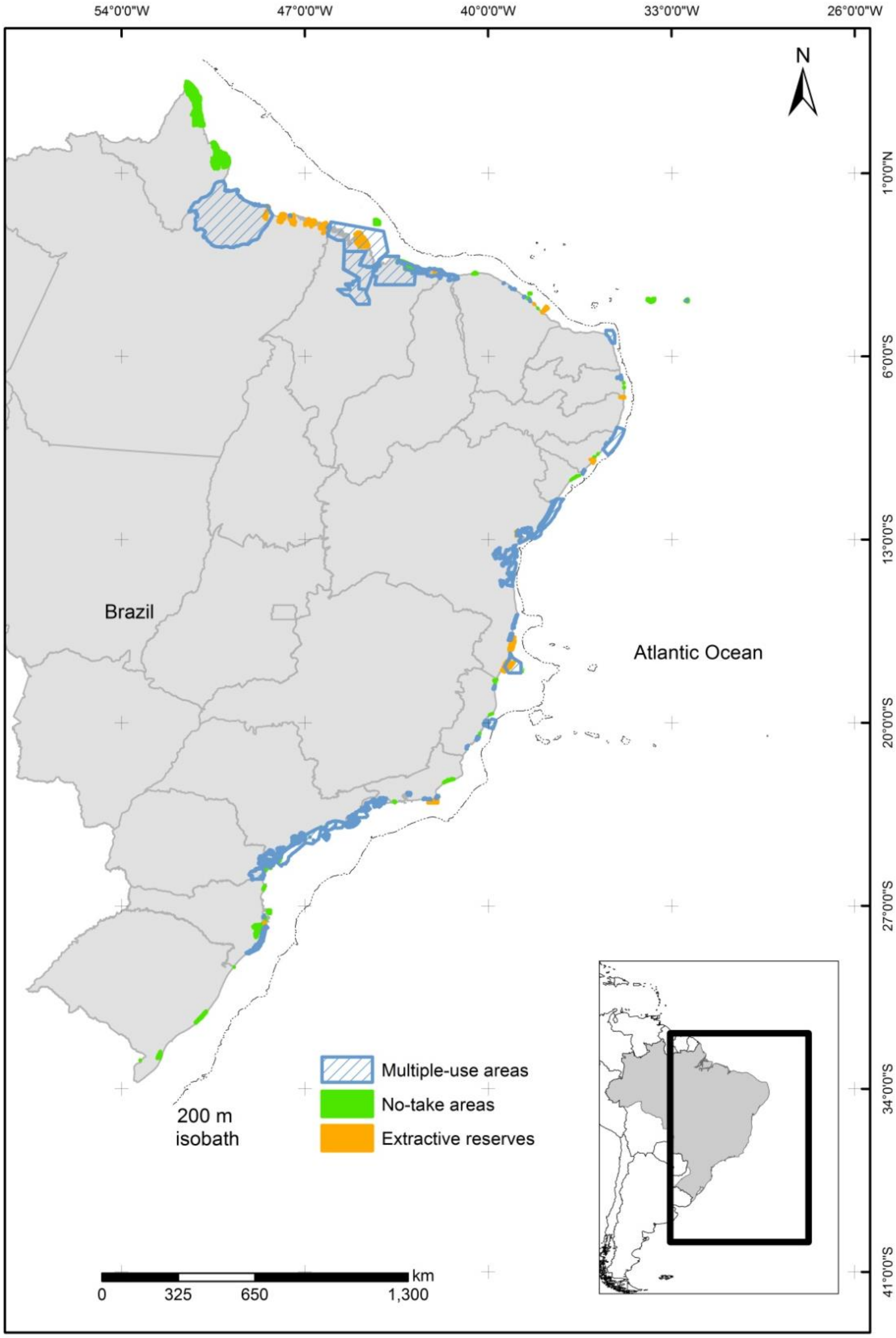

Figure C2.2 Brazilian marine protected areas (MPAs) classified according to their main management categories: no-take areas, extractive reserves, and multiple-use areas.

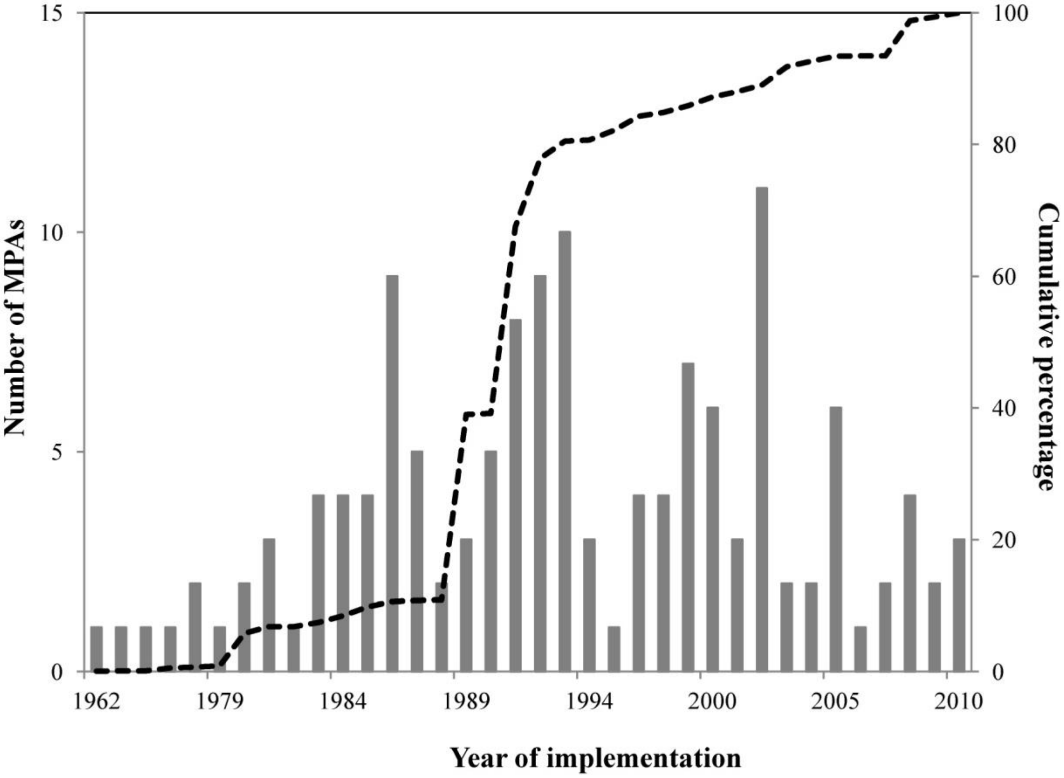

Figure C2.3 Chronological pattern of creation of marine protected areas (MPAs) in Brazil. Bars indicate the number of MPAs (total 142) established by year and are linked to the left-hand axis. The dashed line indicates the cumulative percentage of total extent of established MPAs and is linked to the right-hand axis.

Table C2.1 Coverage (%) of marine habitats by Brazilian MPAs. Abbreviations for ecoregions: Am=Amazon, Nb=Northeastern Brazil, Eb= Eastern Brazil, Fr= Fernando de Noronha and Atoll das Rocas, Ss= São Pedro and São Paulo Islands, Tm= Trindade and Martin Vaz Islands, Sb=Southeastern Brazil, Rg=Rio Grande.

Habitats		No-take areas	Extractive reserve areas	Multiple-use areas
0-10m	Am	2.53	2.52	19.48
	Nb	0.36	0.73	8.81
	Eb	5.13	17.80	23.61
	Fr	68.95	0.00	0.00
	Ss	0.00	0.00	0.00
	Tm	0.00	0.00	0.00
	Sb	2.94	0.56	30.54
	Rg	0.36	0.00	0.19
10-25m	Am	0.57	1.07	18.06
	Nb	0.13	0.90	12.90
	Eb	1.12	3.03	7.30
	Fr	90.72	0.00	0.00
	Ss	0.00	0.00	0.00
	Tm	0.00	0.00	0.00
	Sb	1.40	0.05	49.92
	Rg	0.03	0.00	0.64
25-50m	Am	0.38	0.16	4.03
	Nb	0.00	0.04	20.25
	Eb	0.40	0.08	2.26
	Fr	83.66	0.00	0.00
	Ss	0.00	0.00	0.00
	Tm	0.00	0.00	0.00
	Sb	0.70	0.31	16.95
	Rg	0.00	0.00	1.09
50-75m	Am	0.00	0.04	0.89
	Nb	0.00	0.00	5.38
	Eb	0.00	0.04	0.87
	Fr	62.45	0.00	0.00
	Ss	0.00	0.00	0.00
	Tm	0.00	0.00	0.00
	Sb	0.01	0.54	0.94
	Rg	0.00	0.00	0.04

75-100m	Am	0.00	0.00	0.02
	Nb	0.00	0.00	3.98
	Eb	0.00	0.00	0.50
	Fr	52.17	0.00	0.00
	Ss	0.00	0.00	0.00
	Tm	0.00	0.00	0.00
	Sb	0.00	0.66	0.48
	Rg	0.00	0.00	0.00
>100m	Am	0.00	0.00	0.00
	Nb	0.00	0.00	0.03
	Eb	0.00	0.00	0.04
	Fr	0.05	0.00	0.00
	Ss	0.00	0.00	0.00
	Tm	0.00	0.00	0.00
	Sb	0.00	0.00	0.08
	Rg	0.00	0.00	0.00
coral reef	Am	94.00	0.00	0.00
	Nb	0.81	0.68	30.01
	Eb	65.70	4.41	23.80
	Fr	100.00	0.00	0.00
mangrove	Am	14.95	21.07	54.86
	Nb	0.91	3.28	21.56
	Eb	0.62	14.53	53.54
	Sb	15.19	0.84	51.86

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Appendix C3 – Additional Results for Chapter 3

Database containing 134 studies that were used in this chapter can be found at: http://dx.doi.org/10.1016/j.biocon.2013.12.032.

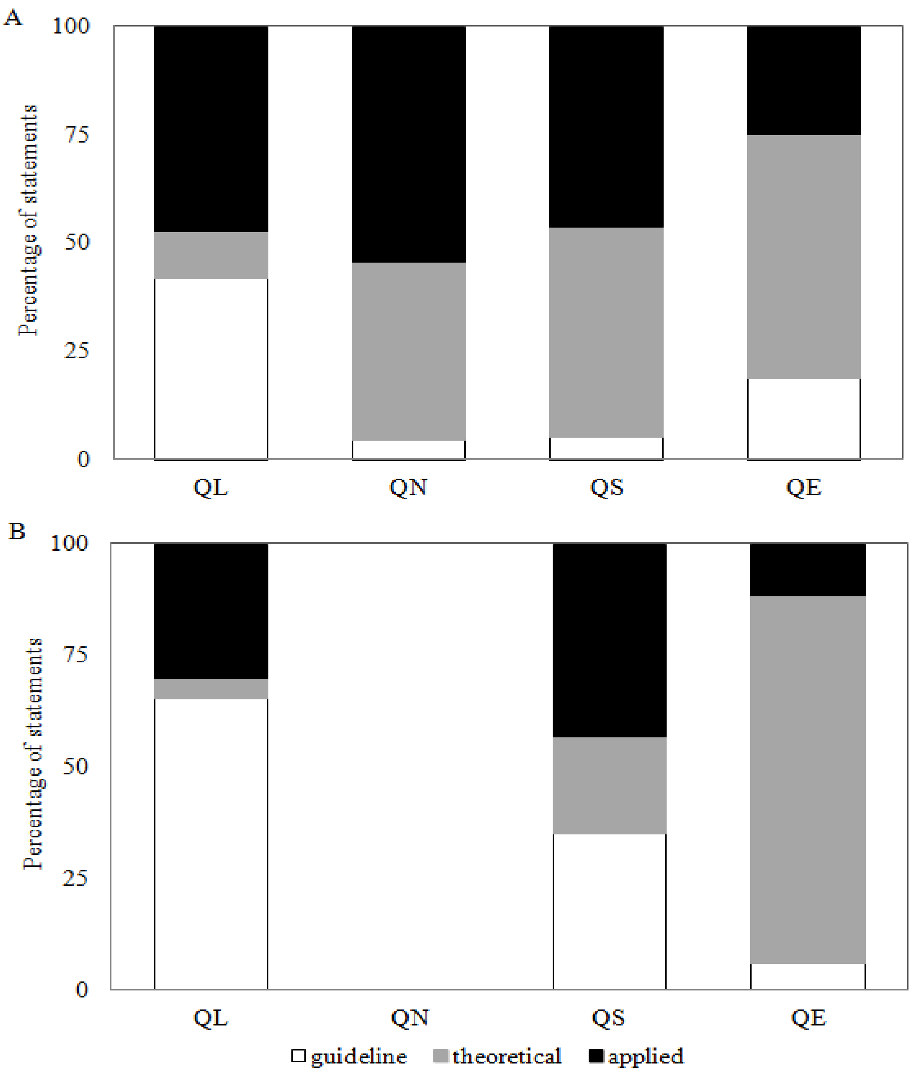

Figure C3.1 Distribution of qualitative statements and each type of quantitative statement among studies with different scopes. A. Statements related to connectivity. B. Statements related to climate change. QL *refers to qualitative statements; QN, quantitative with no rationale; QS, quantitative, subjective; QE, quantitative, justified ecologically. Study scopes are guideline (e.g. reviews), theoretical (e.g. novel approaches or advances), or applied (e.g. supporting government or NGO commitments).*

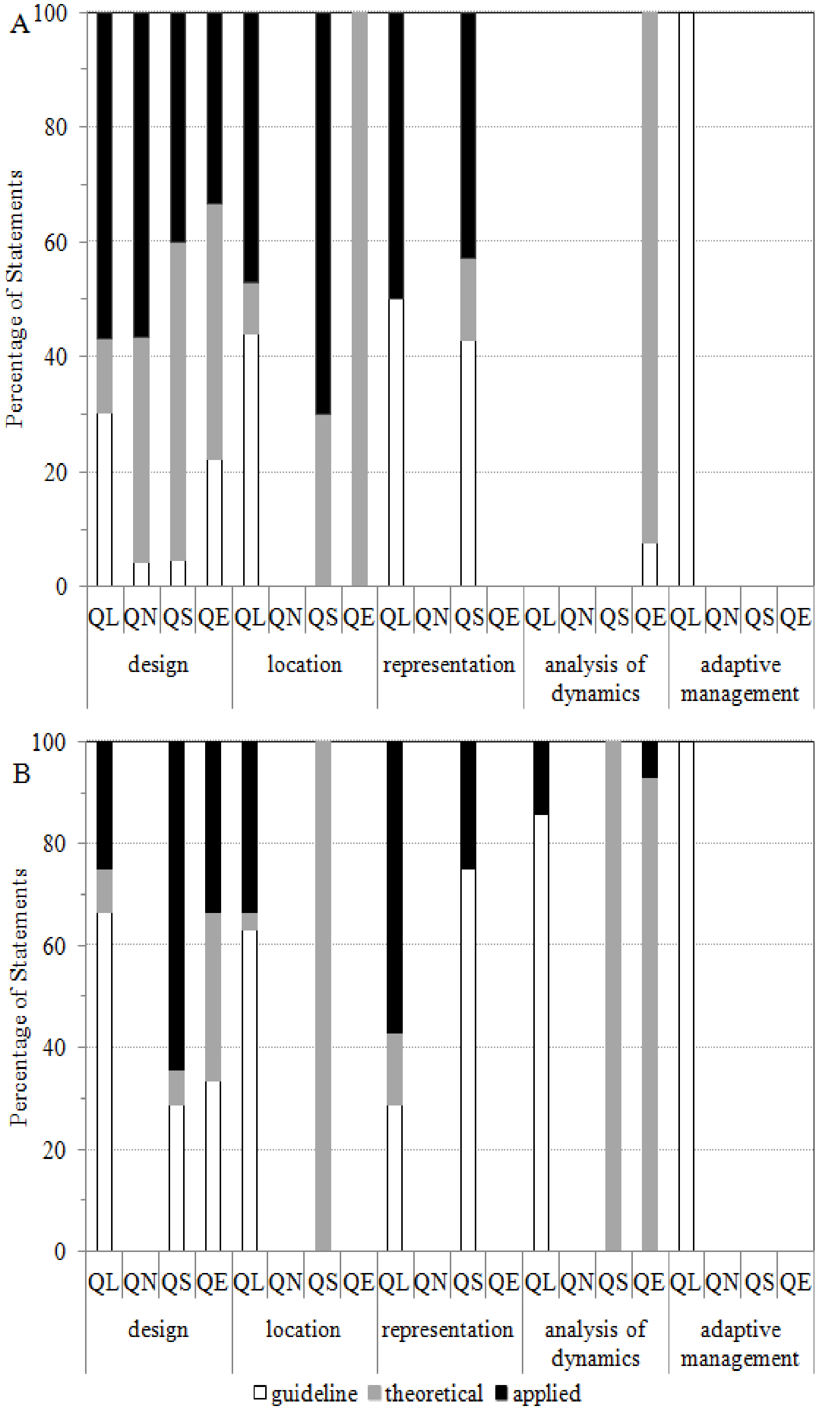

Figure C3.2 Distribution of qualitative statements and three kinds of quantitative statement among categories of statements and scopes of studies. A. Connectivity. B. Climate change. QL refers to *qualitative statements; QN, quantitative with no rationale; QS, quantitative, subjective; QE, quantitative, justified ecologically. Study scopes are guideline (e.g. reviews), theoretical (e.g. novel approaches or advances), or applied (e.g. supporting government or NGO commitments).*

Appendix C4 – Additional Methods and Results for Chapter 4

Habitat quality index details

The single index of relative habitat quality $\boldsymbol{HQI}$ is based on four stressors as described below.

Fishing intensity index

The fishing intensity index was derived from mapping methods originally provided by Rowlands et al. (2012) where the potential impact of the traditional and industrial fisheries was calculated according to Eq. (1) and (2) below.

The reef fishing intensity index $\boldsymbol{RFI}$ was calculated by summing up both artisanal and industrial fishery pressures, normalizing and inverting the resulting values to a range of zero to one (Eq. 3), where the value of one had the lowest fishing potential (therefore highest habitat quality) and zero represented cells under the highest fishing pressure (therefore lowest habitat quality).

$$\boldsymbol{F}_{\mathrm{T}} \quad \sum_{\boldsymbol{i=1}}^{\boldsymbol{426}} \boldsymbol{fd}_{\mathrm{Ti}} \quad (\boldsymbol{P}_{\mathrm{Ti}} \quad \boldsymbol{B}_{\mathrm{T}}) \qquad 1$$

where potential impact of the traditional fishery $\boldsymbol{F}_{\mathrm{T}}$ is a function of $\boldsymbol{fd}_{\mathrm{Ti}}$, a distance decay factor (0−1) derived from the minimum at-sea distance from the centroid of a reef cell to the **i**$^{\mathbf{th}}$ port, $\boldsymbol{P}_{\mathrm{Ti}}$, the number of traditional vessels in the **i**$^{\mathbf{th}}$ port, and $\boldsymbol{B}_{\mathrm{T}}$, the difference in visual sampling efficiency of the traditional sector.

$$\boldsymbol{F}_{\mathrm{I}} \quad \boldsymbol{Z}_{\mathrm{I}}\left(\sum_{\boldsymbol{i=1}}^{\boldsymbol{17}} \boldsymbol{fd}_{\mathrm{Ii}} \times (\boldsymbol{P}_{\mathrm{Ii}} \quad \boldsymbol{B}_{\mathrm{I}} \quad \boldsymbol{E}_{\mathrm{I}})\right) \qquad 2$$

where $\boldsymbol{F}_{\mathrm{I}}$ is the potential impact of the industrial fisheries, $\boldsymbol{Z}_{\mathrm{I}}$ the likely fishing use of a cell based on the depth of the cell, was set equal to 1; $\boldsymbol{fd}_{\mathrm{Ii}}$, $\boldsymbol{P}_{\mathrm{Ii}}$, $\boldsymbol{B}_{\mathrm{I}}$ are the decay factor, number of vessels, and correction factor, respectively; $\boldsymbol{E}_{\mathrm{I}}$ represents the efficiency of industrial vessels relative to traditional vessels.

$$\boldsymbol{RFI} = \frac{[(\boldsymbol{F}_{\mathrm{T}} \quad \boldsymbol{F}_{\mathrm{I}}) \times (\boldsymbol{-1}) + (\boldsymbol{F}_{\mathrm{T}} \quad \boldsymbol{F}_{\mathrm{I}})_{\mathrm{max}} \quad (\boldsymbol{F}_{\mathrm{T}} \quad \boldsymbol{F}_{\mathrm{I}})_{\mathrm{min}}]}{(\boldsymbol{F}_{\mathrm{T}} \quad \boldsymbol{F}_{\mathrm{I}})_{\mathrm{max}}} \qquad 3$$

where $(\boldsymbol{F}_{\mathrm{T}} \quad \boldsymbol{F}_{\mathrm{I}})_{\mathrm{max}}$ is the maximum combined score for a reef cell in the study region.

Google Earth Pro was used to calculate potential impact of the fisheries on coral reef cells by identifying 3,610 traditional and 65 industrial active vessels in 429 fishing ports or fish landings throughout study region (images spanning 2001-2011). Fishing vessels were distinguished between traditional and industrial categories by their length; traditional vessels are typically 6-12 m long while industrial ones are > 15m. I admitted some flexibility in those values due to regional differentiation in fleet characteristics, following fishery surveys (Brasil 2004, Brasil 2005, Brasil 2008). Paddled canoes (typically <5 m) identified inside estuaries were excluded from the analyses because this simple technology restricts fisher mobility. To define the maximum distance beyond which reef cells were deemed not to be fished by traditional vessels, I used a varying linear decay model in accordance with the location of the fishing port as reported in Brasil (2004), Brasil (2005), Brasil (2008). This maximum distance varied from 60 to 180 km offshore. $\boldsymbol{B}_{\mathrm{T}}$ used here was 2.7 (roughly 9,600 vessels identified during fishing survey [Brasil 2008]). When calculating the potential impact of industrial fisheries, the term $\boldsymbol{Z}_{\mathrm{I}}$ in Eq. (2) was equal to 1 because data about the likely fishing use of a reef cell based on the depth of the cell was not available. Similarly to maximum distance in the artisanal fishery model, I allowed the linear decay model to be varied geographically. The maximum distance in which a cell could be fished corresponded to the width of continental shelf. Because 200 industrial vessels are registered for the region (Brasil 2008), $\boldsymbol{B}_{\mathrm{I}}$ equalled 3.07. Based on recent statistics of fishery landing (Brasil 2010), I estimated $\boldsymbol{E}_{\mathrm{I}}$ to be 14.2.

Thermal stress index

I examined the spatial pattern of thermal stress based on the index of acute stress Degree Heating Weeks (DHW), the most influential predictor of coral bleaching. The DHW is calculated from accumulating HotSpots of ≥1 °C that occur during a 12-week window, where a HotSpot is defined as the temperature above the maximum of the monthly mean (Skirving et al. 2006). To estimate the long-term pattern of heat stress across the study region, time series data of DHW from 1985-2009 were obtained from the freely available National Oceanic and Atmospheric Administration (NOAA) Advanced Very High Resolution Radiometer (AVHRR) sensor series. Annual maximum DHWs were calculated for each coral reef cell and averaged over the 25-year time period. Thermal stress index $\boldsymbol{TSI}$ was expressed as the ratio to the maximum score in the study region and inverted so that cells with a value of zero were under high thermal stress, while a cell with a value of one indicated low thermal stress.

$$\boldsymbol{TSI} = \frac{[(\boldsymbol{DHW}) \times (-\mathbf{1}) + (\boldsymbol{DHW})_{\max} \quad (\boldsymbol{DHW})_{\min}]}{(\boldsymbol{DHW})_{\max}} \qquad 4$$

where $\boldsymbol{DHW}$ is the mean of annual maximum Degree Heating Weeks to which a given reef cell experiences and $(\boldsymbol{DHW})_{\max}$ is the maximum score in the dataset for the study region.

Water clarity index

This index was based on the diffuse attenuation coefficient at 490 nm (K490), which is an indicator of water clarity. The value of K490 represents the rate at which light intensity at 490 nm is attenuated with depth. The water clarity index thus provides an assessment of optical properties representative of coastal regions displaying terrestrial input influences in delivering organic matter to aquatic ecosystems (Andrew et al. 2013). Those values were retrieved and spatially subset from MODIS Aqua monthly averages satellite image during 2003-2011 employing the Giovanni online data system through the website http://gdata1.sci.gsfc.nasa.gov/daac-in/G3/gui.cgi?instance_id=ocean_8day. The index is computed as $\boldsymbol{WCI}$ where $\boldsymbol{WCI}_{\mathrm{K}}$ is the rate m^{-1} in which visible light is extinguished as it passes down the water column, measured for each reef cell, and $(\boldsymbol{WCI}_{\mathrm{K}})_{\max}$ represents the maximum value across the study region. I also rescaled the measures to a zero (lowest water clarity, poorest quality habitat) to one (highest water clarity, best quality habitat) scale.

$$\boldsymbol{WCI} = \frac{[(\boldsymbol{WCI}_{\mathrm{K}}) \times (-\mathbf{1}) + (\boldsymbol{WCI}_{\mathrm{K}})_{\max} \quad (\boldsymbol{WCI}_{\mathrm{K}})_{\min}]}{(\boldsymbol{WCI}_{\mathrm{K}})_{\max}} \qquad 5$$

Coastal development index

The coastal development index was calculated as originally proposed Rowlands et al. (2012), whose index is measured by a distance from night time lights emission provided by the Defense Meteorological Satellite Program (DMSP) produced at the National Oceanic & Atmospheric Administration, National Geophysical Data Center (NOAA/NGDC) and collected by US Air Force Weather Agency. Night time lights are a proxy measure for associated human-caused stressors (Aubrecht et al. 2008). The present metric $\boldsymbol{LPI}$ (light proximity index) assumes a greater impact can be expected for reefs situated in close proximity to a source of high night light intensity, than those found more distantly (Rowlands et al., 2012). Sensitivity analyses were used to evaluate how results changed when using different input radii as the maximum distance from the centroid of a given reef cell as suggested by Rowlands et al. (2012). I then applied the threshold of 25 km when calculating the exposure of reef cells to the coastal development index $\boldsymbol{CDI}$ (Eq. 6). This formulation assumes that there is no harmful impact from terrestrial industry or domestic housing on a coral reef located at sites further than 25 km. $\boldsymbol{CDI}$ was also rescaled from zero to one where a reef cell with a value of 0 means most intense light source and one means no light measured within 25 km.

$$\boldsymbol{CDI} = \frac{[(\boldsymbol{LPI}) \times (-\mathbf{1}) + (\boldsymbol{LPI})_{\max} \quad (\boldsymbol{LPI})_{\min}]}{(\boldsymbol{LPI})_{\max}} \quad 6$$

Where $\boldsymbol{LPI}$ is the $\boldsymbol{LPI}$ calculated for a given reef cell and $(\boldsymbol{LPI})_{\max}$ is the maximum value registered for any cell in the study region.

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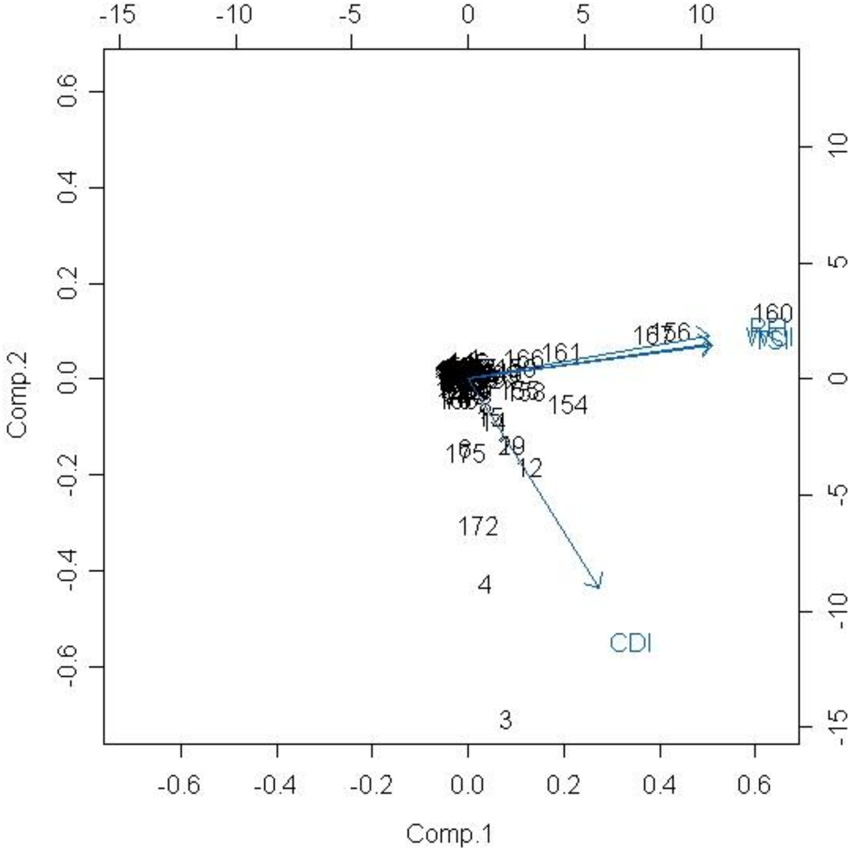
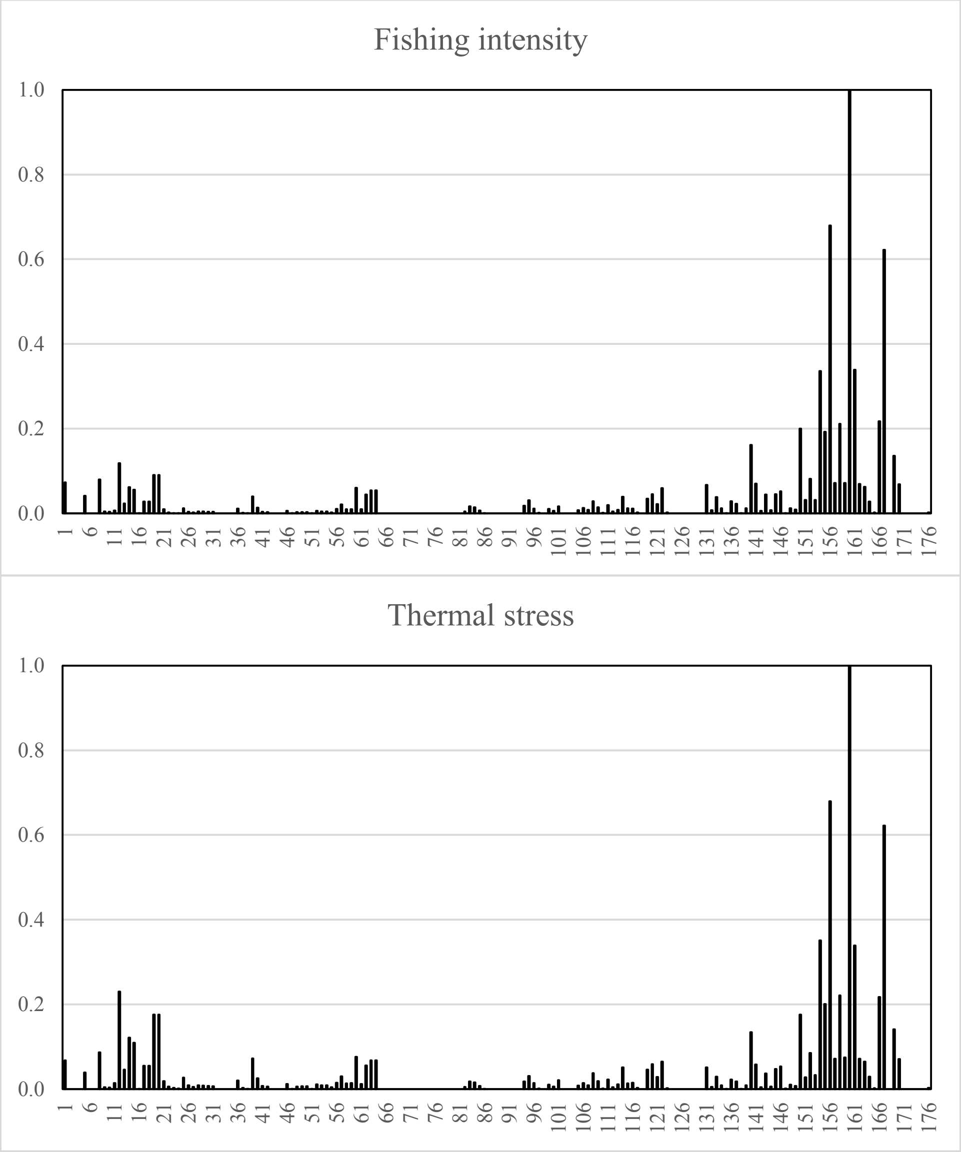


Figure C4.1 Principal components analysis (PCA) showing correlation between four stressors across 176 reef cells: fishing intensity (RFI), thermal stress (TSI), coastal development (CDI), and sedimentation (WCI). I observed that most of the reef cells clustered together for all stressors but partial separation occurred for CDI in some reef cells. Overall, heavily-fished reefs are also those located near cities, where they are exposed to increased sediment load, and experience high thermal stress, making them highly vulnerable to human effects.


Fishing intensity
1.0
0.8
0.6
0.4
0.2
0.0
1
6
11
16
21
26
31
36
41
46
51
56
61
66
71
76
81
86
91
96
101
106
111
116
121
126
131
136
141
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151
156
161
166
171
176
Thermal stress
1.0
0.8
0.6
0.4
0.2
0.0
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6
11
16
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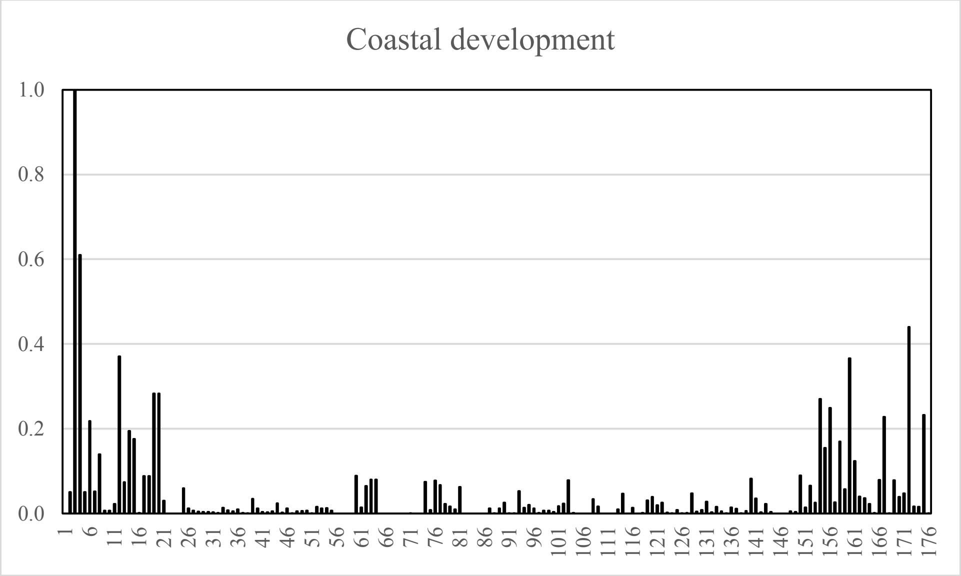

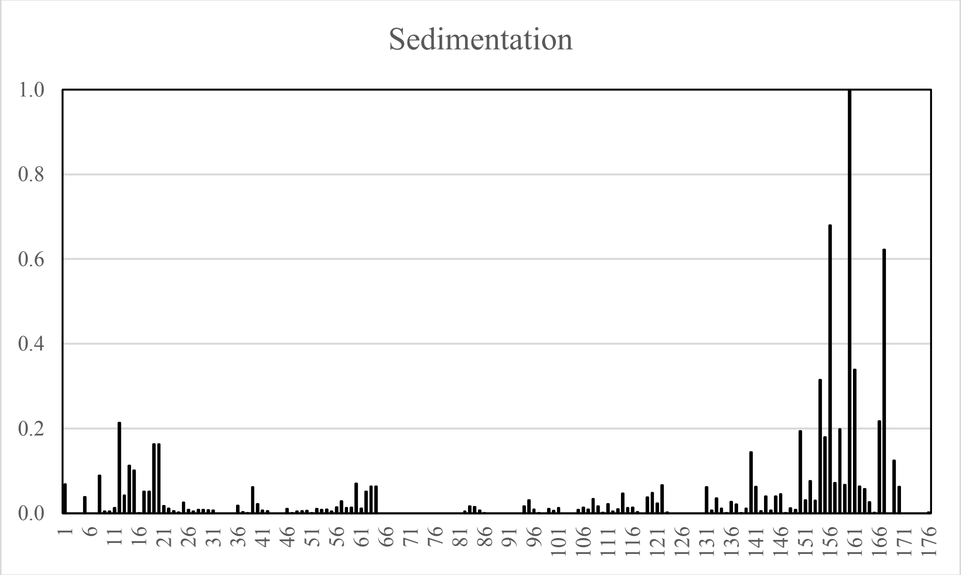

Figure C4.2 Histograms depicting habitat quality information for 176 reef cells based on each of the stressors separately. Numbers on the x-axes (0-1) indicate the predicted coral-reef state ranging from the poorest quality (0: heavily fished, subjected to high thermal stress, closest to large human communities, or having poorest water quality) to the best quality habitat (1: lowest fishing potential, low thermal stress, further away from large human communities, or highest water quality).

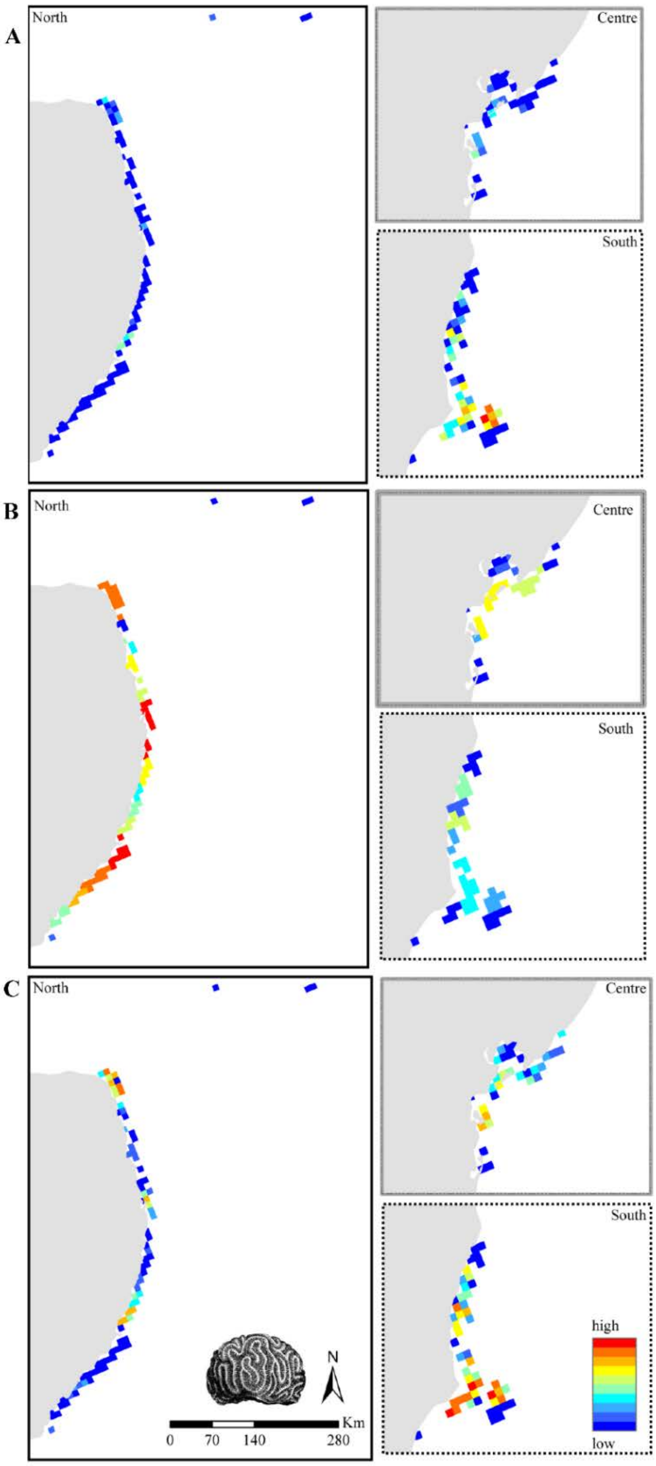

Figure C3.3 Spatial distribution of connectivity metrics for the broadcasting coral in Brazil: (A) out-flux, (B) betweenness centrality, and (C) local retention.

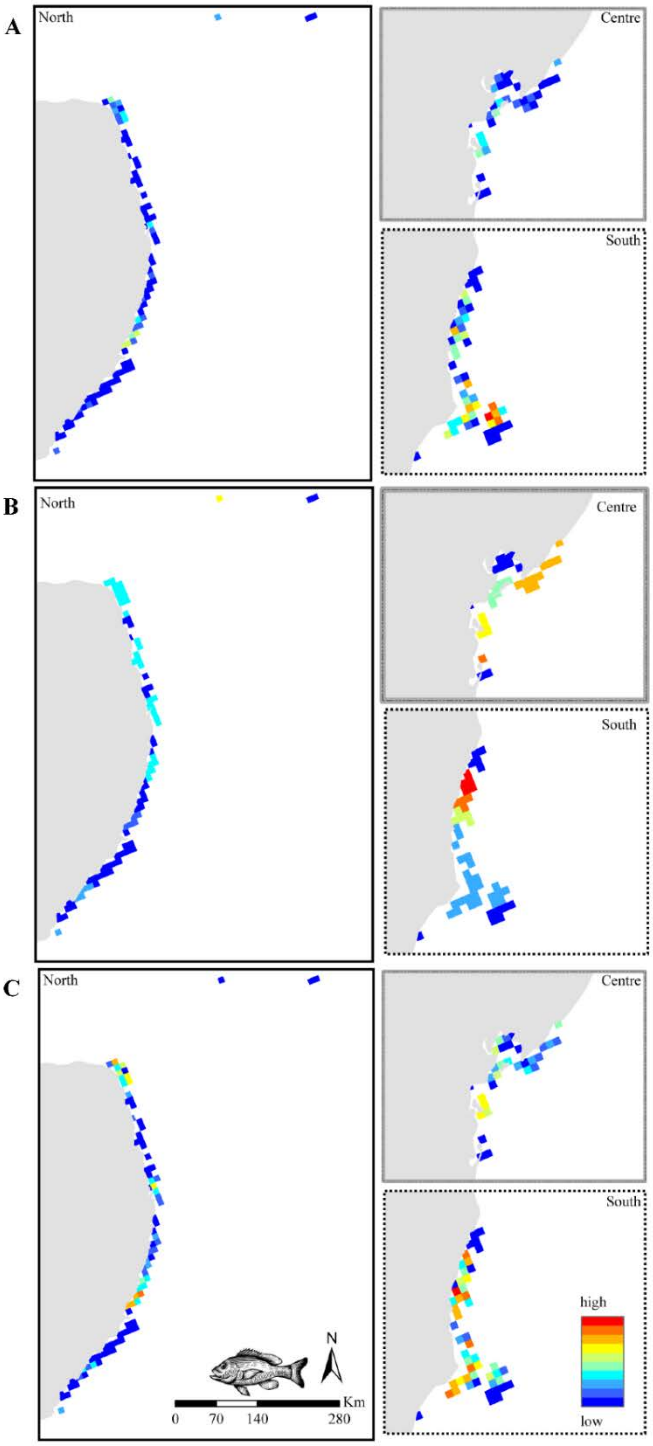

Figure C3.4 Spatial distribution of connectivity metrics for the snapper in Brazil: (A) out-flux, (B) betweenness centrality, and (C) local retention.

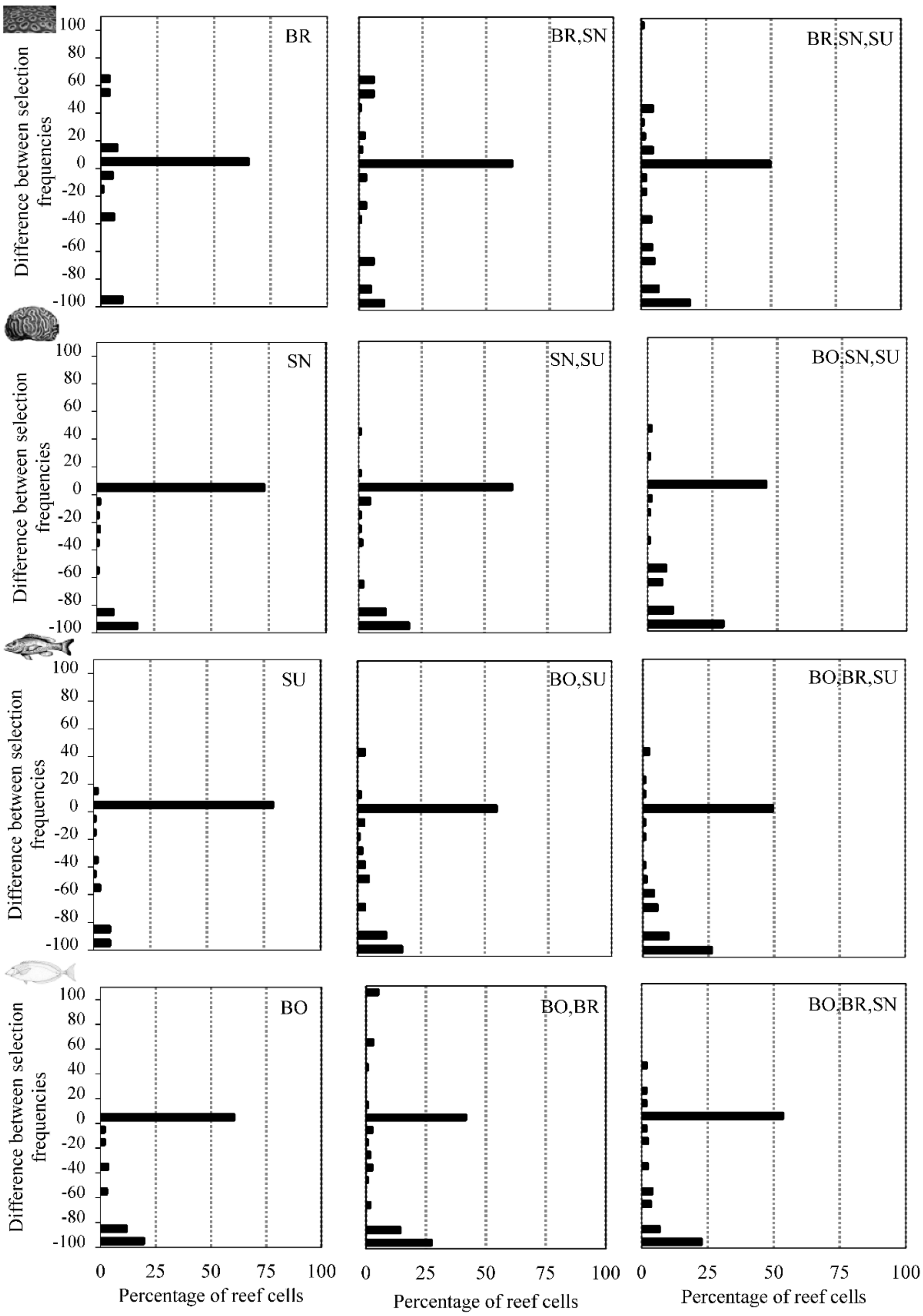

Figure C4.5 Differences in selection frequencies of reef cells between scenarios when different combinations of species were considered. From left to right, the panels show the effect of increasing the number of conservation features with the addition of one, two, and three species, respectively, with their metrics. Comparisons were made *against scenarios including only one individual focal species (from top to bottom, respectively): brooder coral (BO), broadcasting coral (BR), snapper (SN), and surgeonfish (SU). I then subtracted the selection frequency of each reef cell derived from single species scenarios from the selection frequency of scenarios that included progressively more species, to evaluate spatial differences in priority areas.*

*Table C4.1 Results of ANOVA and post-hoc tests for the effectiveness of multi-species matrices at achieving connectivity for individual species across 100 runs for each combination of metric and species. BO, brooder coral; BR, broadcasting coral; SN, snapper; SU, surgeonfish; MS1, multi-species approach using the inclusive method; MS2, multi-species approach unsing the strict method; MS, mean squares; F, variance ratio; degrees of fredom = 1; *P<0.001.*

		MS1			MS2		
		MS	F	Post-hoc Tukey test	MS	F	Post-hoc Tukey test
Out-flux	BO	63.60	2.59	-	26.15	0.35	-
	BR	18.65	1.16	-	36.27	2.51	-
	SN	55.43	0.92	-	48.31	4.92	-
	SU	11.87	1.33	-	53.25	5.21	-
Betweenness centrality	BO	145.5	11.32*	MS1>BO	166.75	11.98*	BO>MS2
	BR	123.27	8.52*	MS1>BR	138.08	8.21*	BR>MS2
	SN	58.79	6.46*	SN>MS1	38.71	2.12	-
	SU	86.95	7.86*	MS1>SU	43.13	3.75	-
Local retention	BO	77.85	3.94*	BO>MS1	25.17	2.89	-
	BR	66.97	12.38*	BR>MS1	59.31	5.85	-
	SN	61.52	6.01	-	133.27	8.52	MS2>SN
	SU	78.47	8.31	SU>MS1	63.22	5.94	-

Appendix C5 – Additional Methods and Results for Chapter 5

Description of methods involved in the bias correction and downscaling.

Global projection of SST are produced at a coarse resolution and might over-represent SST means. I followed the method described by Dunne et al. (2013) for bias correction through downscaling that will enable planners to undertake a conservation planning that is more informed. As standards for comparisons between actual and modeled SST in the validation procedures, I used monthly records for SST observational data obtained from NOAA AVHRR and hindcasts for GCM PCM1 outputs for a previous ―training period” (1985–1999) of 20th century simulations (20C3M). Initially, I generated a monthly climatology for both NOAA and PCM1 and calculated the difference between the maximum of each climatology as an anomaly to develop the mean-corrected SST, or SST^{MC}. Rather than using binned SST data on a decadal scale, as originally suggested by Dunne et al. (2013), I calculated the climatological data for 5-year periods of time because the training period spanned only 15 years. To normalize PCM1 variability to observations over the entire retrospective (the training period) and projected time frames, I calculated annual maximum SST (SST^{AM}) and then the moving 5-year mean maximum SST (as 5-year-box-car smoothed values of), inserting median values into the start and end years of these periods. The variance-corrected SST (SST^{VC}) was calculated with the following expression:

$$SST^{VC} = SST^{MC} - (SST^{AM} - SST^{TM}) \times (1 - SST^{NOAA\_GCM} / SST^{GCM}) \quad 1$$

where, SST^{MC} is a mean-corrected SST (difference between the maximum for each climatology), SST^{AM} is the annual maximum, SST^{TM} is the moving 5-year mean maximum, SST^{NOAA_GCM} and SST^{GCM} are the single 5-year maximum anomaly estimates for both NOAA and GCM datasets, respectively. These latter anomalies are the differences between the 5-year maximum and the climatological maximum for the 5-year periods. Anomalies were averaged to produce a single value for each dataset. Averages were applied only to those reef cells where SST^{NOAA_GCM}/SST^{GCM} was less than one to avoid adding variability where NOAA gave more variability than GCM. For model validation, I compared the climatology for the –training period” (1985-1999) provided by PCM1 and actual satellite data. I determined the correlation between predicted and observed SST values in a pairwise comparison. Values for Spearman correlation ranged from 0.7321 and 0.9875 (mean = 0.9237, median = 0.9058) with p-value < 0.005 (see Figure C5.1 for the correlation values for five reef cells).

Reference

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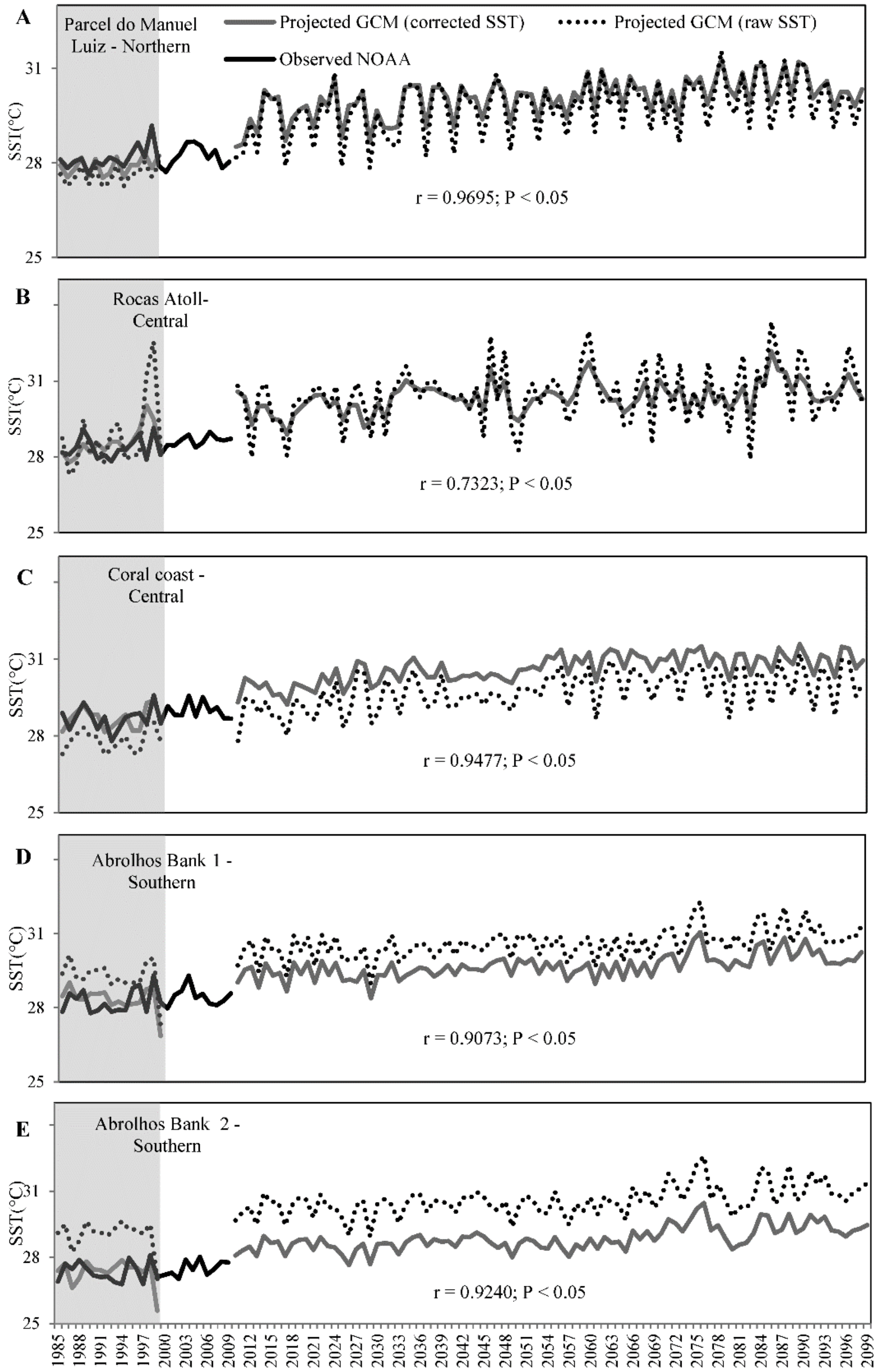
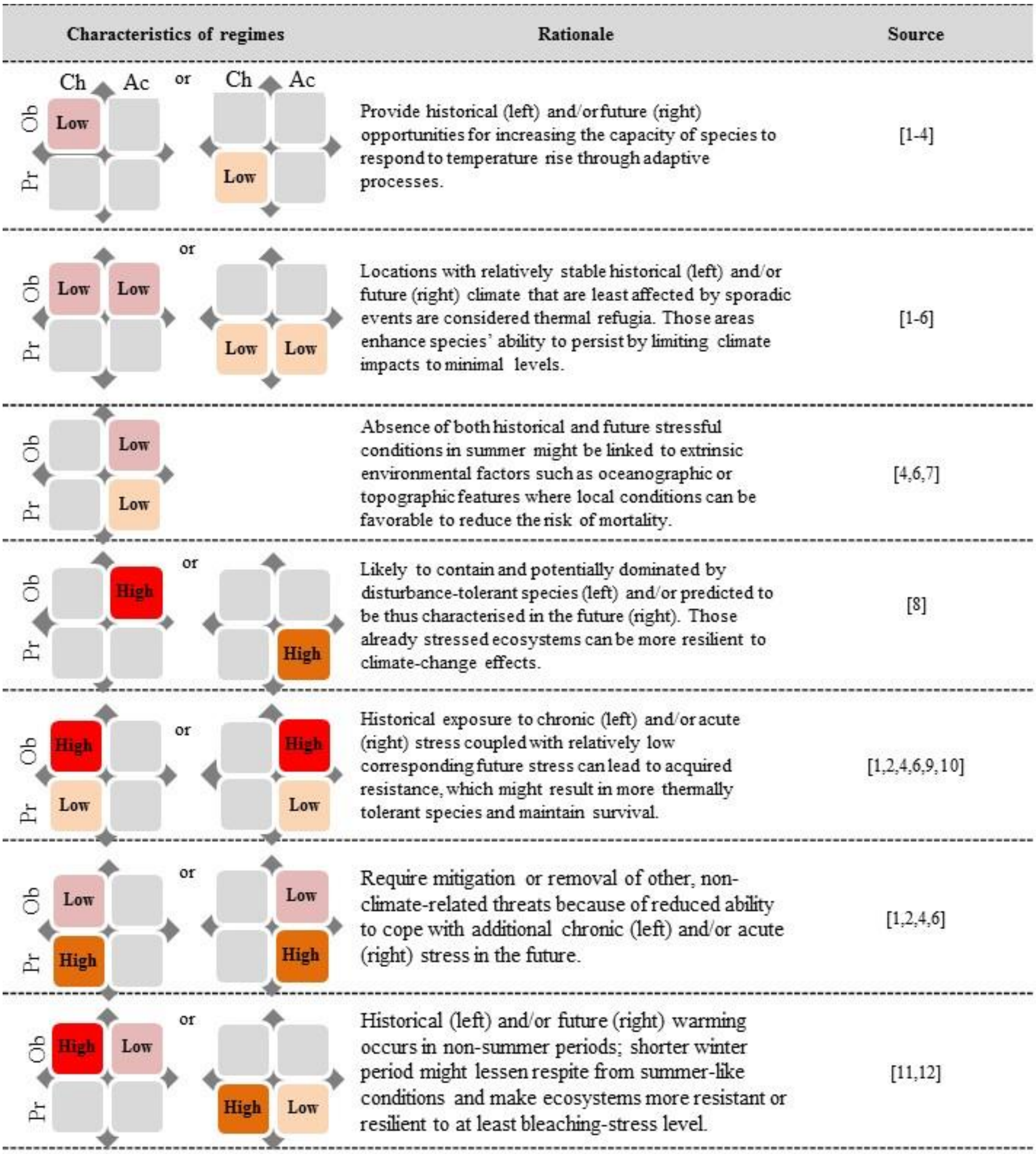


Figure C5.1 Annual maximum SST for five reef cells across study area. Observed data (satellite NOAA) are shown by solid lines in black (1985-2009) while projections are shown by dotted lines for raw GCM PCM1 output and solid lines in gray after *bias removal (corrected values). Approximate locations of the five cells (a-e) are shown as in Fig. 2A. Spearman correlation (r) between annual maximum SST from satellite data and PCM1 after bias removal for the "training period" (1985–1999, indicated by the shading area in the graph) are presented for five reef cells.*



Characteristics of regimes	Rationale	Source
Ob Ch: Low or Pr Ch: Low	Provide historical (left) and/or future (right) opportunities for increasing the capacity of species to respond to temperature rise through adaptive processes.	[1-4]
Ob Ch: Low, Ob Ac: Low or Pr Ch: Low, Pr Ac: Low	Locations with relatively stable historical (left) and/or future (right) climate that are least affected by sporadic events are considered thermal refugia. Those areas enhance species' ability to persist by limiting climate impacts to minimal levels.	[1-6]
Ob Ac: Low, Pr Ac: Low	Absence of both historical and future stressful conditions in summer might be linked to extrinsic environmental factors such as oceanographic or topographic features where local conditions can be favorable to reduce the risk of mortality.	[4,6,7]
Ob Ac: High or Pr Ac: High	Likely to contain and potentially dominated by disturbance-tolerant species (left) and/or predicted to be thus characterised in the future (right). Those already stressed ecosystems can be more resilient to climate-change effects.	[8]
Ob Ch: High, Pr Ch: Low or Ob Ac: High, Pr Ac: Low	Historical exposure to chronic (left) and/or acute (right) stress coupled with relatively low corresponding future stress can lead to acquired resistance, which might result in more thermally tolerant species and maintain survival.	[1,2,4,6,9,10]
Ob Ch: Low, Pr Ch: High or Ob Ac: Low, Pr Ac: High	Require mitigation or removal of other, non-climate-related threats because of reduced ability to cope with additional chronic (left) and/or acute (right) stress in the future.	[1,2,4,6]
Ob Ch: High, Ob Ac: Low or Pr Ch: High, Pr Ac: Low	Historical (left) and/or future (right) warming occurs in non-summer periods; shorter winter period might lessen respite from summer-like conditions and make ecosystems more resistant or resilient to at least bleaching-stress level.	[11,12]

Figure C5.2 Characteristics of thermal-stress regimes. Regimes are made up of different combinations of metrics for chronic (Ch) and acute (Ac) stress derived from observed (Ob) and projected (Pr) time-series. Based on supporting literature, rationales for their conservation are presented.

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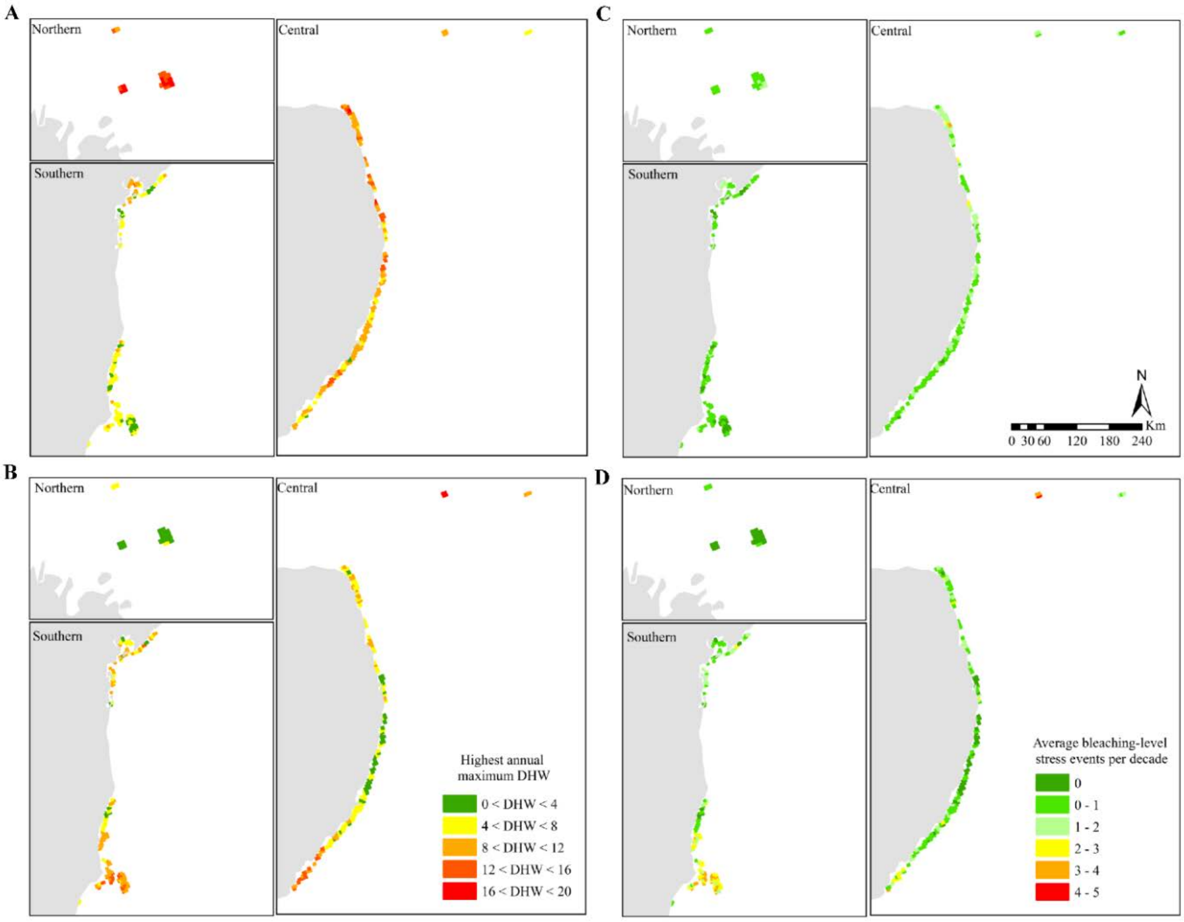


Figure C5.3 Intensity and frequency of bleaching-level stress (acute) events. The highest annual maximum DHW based on observed (A) and projected (B) SST values as an indicator of intensity of acute events. Average number of bleaching-level stress events (when DHW > 4) per decade as an indicator of the frequency of acute events, derived from observed (C) and projected (D) SST time-series. Views for reefs in the north, centre, and south of the study area correspond to insets in Fig. 2A.

Table C5.1 Descriptive statistics for all metrics used to formulate thermal stress regimes

	Chronic/Observed	Acute/Observed	Chronic/Projected	Acute/Projected
First tercile	**0.414**	**0.080**	**0.276**	**0.056**
Third tercile	**0.544**	**0.267**	**0.580**	**0.171**
Mean	**0.511**	**0.212**	**0.475**	**0.163**
Median	**0.482**	**0.132**	**0.501**	**0.098**

Appendix C6 – Additional Methods and Results for Chapter 6

Biodiversity data

Biodiversity features were summarized within 1 km^2 reef cells (n=2,276), which could be selected for protection based on its contribution to my conservation objectives.

Ecosystem delineation

The ecosystem delineation approach had four levels: (i) four ecoregions (i.e., Amazon, Northeastern, Eastern, and Fernando de Noronha and Atol das Rocas), (ii) six geomorphologic types (nearshore bank, bank off the coast, fringing, patch, mushroom reef, and atoll), (iii) two depths (deep and shallow), (iv) and two tidal zone classes (subtidal and intertidal). Because not all combinations were present, I stratified coral reefs into 23 classes, each of which had a conservation objective to be achieved.

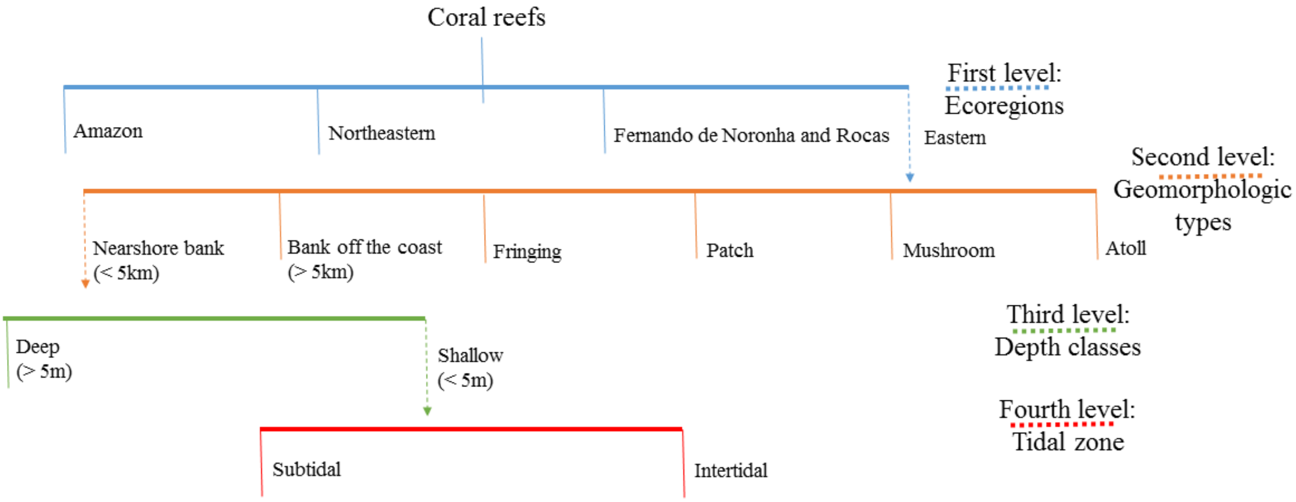


Figure C6.1 Hierarchical classification scheme for delineation of ecosystem types.

The coral reef locations and areas were primarily derived from mapping procedures with the use of Landsat 5 ETM+ satellite imagery at 30-m spatial resolution (Brasil, 2006). This mapping was supplemented by the use of satellite images with very high spatial resolution (multispectral IKONOS; spatial resolution of 4 meters), which allowed me to detect the occurrence of smaller reefs (i.e., isolated submerged mushroom reefs/coral pinnacles up to 50 meters in diameter) in the southern part of the study area, where this reef type is present (Kikuchi et al., 2010). Visual interpretation of the satellite imagery and analyses were completed in ArcGIS 10 to delineate all reef polygons.

I first partitioned the reef polygons drawn in ArcGIS by ecoregion into the following: (i) Amazon, (ii) Northeastern, (iii) Eastern, and (iv) Fernando de Noronha and Atol das Rocas. In addition to the delineation of ecoregion boundaries, the characteristics and spatial arrangement of the reef polygons relative to each other was used to allocate them into discrete geomorphologic types within each ecoregion in accordance with Leão and Dominguez (2000), Leão and Kikuchi (2005), Kikuchi et al. (2010): (i) nearshore bank, which comprises small discontinuous reef structures, adjacent to the beach (<5km off shore), and has variable but often elongated forms; (ii) banks off the coast, which have widely variable sizes (<10km or >20km) and shapes (elongated, circular, semi-arched) but are much further from the coastline (>5 km); (iii) fringing reefs, which occur bordering the shores of coastal or oceanic islands; (iv) patch reefs, which are isolated and usually link bank reefs; (v) isolated open-sea coral pinnacles, usually with a diameter of up to 50m; and (vi) one small atoll named Atol das Rocas. A high-resolution spatial depth model (Becker et al., 2009) was used to further subdivide each geomorphologic type within ecoregion into deep (>5m) and shallow (<5m) reefs. The final level of classification defined reef polygons according to the tidal zone. Mapped reefs whose tops were completely exposed in the satellite images were assigned as intertidal reefs; the remaining parts were designated as subtidal reefs. By categorizing the mapped reefs into such spatial framework, I assumed that these 23 unique classes of ecosystem types encompassed multiple habitats subjected to similar exposure regimes of currents, waves, sedimentation, and other physiographic drivers.

Fish species data

I obtained species distribution data for 405 species of reef fish from a geographic range data set compiled by Vila-Nova et al. (2014). In this data set, distribution data were compiled based on a literature review and researchers‘ personal databases and evaluated by experts. The extent of occurrence of each species was clipped by bathymetry to produce a more realistic estimation of their range distributions.

Connectivity data

By simulating the larval dispersal in sea currents, asymmetric connectivity-probability matrices were used to calculate the following metrics for each modeled species: (i) outflux, which is related to the source strength of a reef and thus able to sustain the populations of surrounding reefs through its outgoing connections; (ii) betweenness centrality, which is related to stepping-stone reefs, can control the flux, and help spread the risk against disturbances; and (iii) local retention, which is associated with the degree to which a reef can self-sustain in isolation and hence is important to be protected. These connectivity metrics were summarized for each reef cell in a grid-based model with 176 reef cells (10 x 10 km).

Due to a lack of connectivity information for offshore bank reefs in the very north of the study area (from 0° to 3°S), and given that those reef cells (n = 7) seem to harbor an isolated unique coral community from elsewhere in the southern Atlantic Ocean (Castro and Pires, 2001), I assumed that coinciding reef cells are of the greatest importance for connectivity, and these were given the highest values after normalization for all connectivity metrics.

Climate warming data

By using measures of thermal stress metrics (chronic and acute) and combining historical and projected sea-surface-temperature data, nine thermal stress regimes across the study area were identified. Conservation objectives that tackle protection against climate-related disturbances were formulated to combine any of the following: (i) areas least affected or projected to face minimal thermal stress; (ii) areas providing the greatest opportunities to improve the capacity of coral reefs for adaptive responses to increases in temperatures (low chronic stress only); (iii) sites that have gained resistance to overall stress because historical exposure does not persist; (iv) areas required to manage local stress because thermal stress is projected to increase in the future; and (v) sites containing or projected to contain disturbance-tolerant species. By using measures of chronic and acute thermal stress and combining historical and projected data sets, nine thermal stress regimes occurred across the study area and warranted conservation attention as a way to tackle protection against climate-related disturbances. I then assigned reef cells (grid-based at a scale of 4 x 4 km) to each occurrence of these regimes (i.e. climate-change conservation features).

Conservation objectives

The objectives for ecosystem types ranged from 10-30% of their distribution, depending on the spatial scale of their extension within the study area. For each of the 23 ecosystem types, I set area-based objectives in which 10% corresponds to those with an extension greater than the third quartile of the total area, and 30% to those with an extension smaller than the first quartile. All remaining values were assigned based on linear interpolation between the upper and lower boundaries. Zone-specific targets were set as one third of the overall target as no-take MPAs accordingly.

Similarly, the representation objective coverage for the 79 functional groups was set to guarantee a minimum theoretical value of 10% and a maximum of 30%. The objectives were equally divided among the three biological attributes and then summed to calculate the overall conservation objective for each functional group (Fig. S2). I scaled the targets depending on the number of classes within each attribute such that greater targets would be associated with characteristics that reflect increased vulnerability and with greater population declines. For example, body size had four classes (large, medium, medium-small, small) so the smallest objective was set up as 3.33 and the ratio of increments within this attribute was 2.22 (therefore, the most demanding objective would reach 10%). Maximum depth had five classes and ratio of increment of 1.66 and trophic category had six classes and thus the smallest ratio of increment (1.33).

Gradient of percentages for the objectives was intended to reflect vulnerability to threats. Large-bodied fish species are often prone to fishing pressure and are disproportionally more affected by exploitation (Genner et al., 2010). Similarly, maximum depth influences the extent of vulnerability of fish species because shallow habitats have been shown to be more critical to population decline following reef degradation (Bellwood et al., 2004; Munday, 2004). Finally, trophic category increases the likelihood of coral reef fish population decline and mediates conservation requirements, with obligate sessile invertivores (corallivores) declining proportionately more than others (Muillot et al., 2013). The overall target then ranged from 11.3% to 28.7%. The zone-specific target was set as one third of the overall target within no-take MPAs.

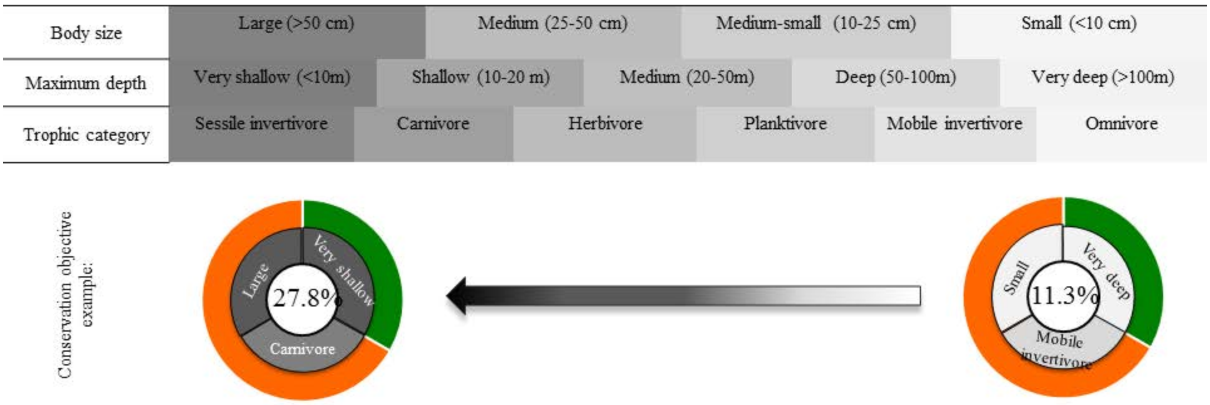
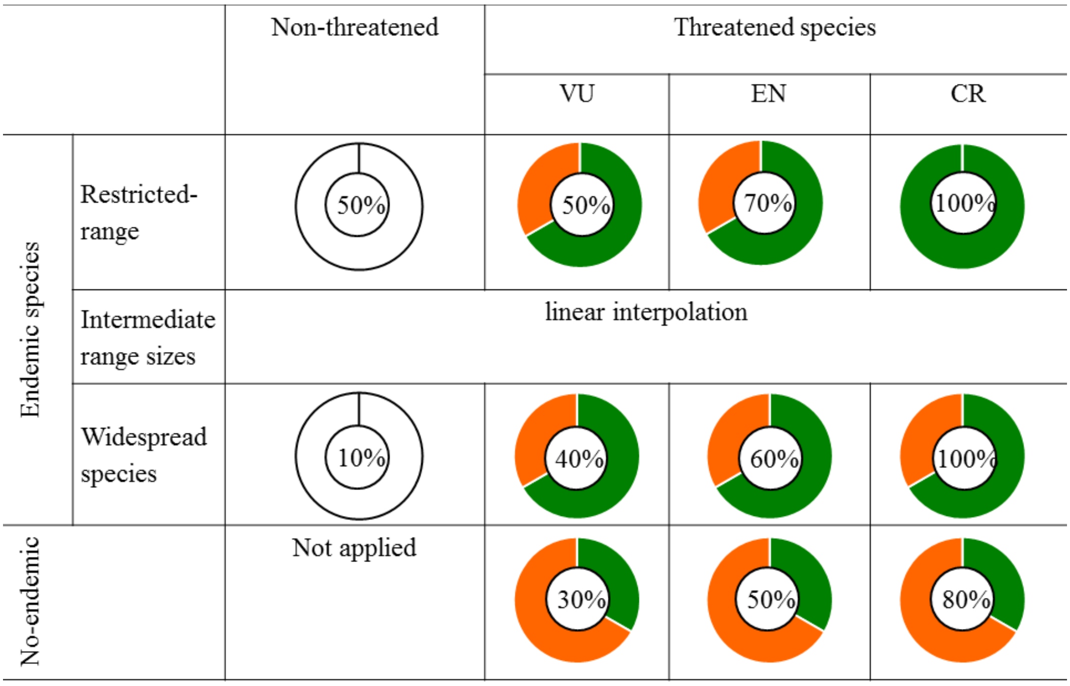


Figure C6.2 Formulation of conservation objectives for functional diversity. Biological attributes (body size, maximum depth and trophic category) for 405 fish species were summarized according to a gradient to reflect their vulnerability to threats (represented by the gray shading) with larger species, associated with shallow habitats and obligate corallivorous having a more demanding objective (dark gray). Conservation objective examples are shown for the minimum and maximum percentage of coverage (inner circle) – i.e. 11.3 and 27.8%, respectively. The proportion of the objective required as no-take or multiple-use zones are illustrated by the size of outer circle (green indicates the coverage required by no-take MPA, i.e. – one third of the overall objective, and orange the remaining objective, optionally required to be achieved by no-take or multiple-use).

For threatened and endemic species, I stipulated that the objectives be inversely scaled with the species geographic range size and directly incremented according to their conservation status (Fig. S3). The representation objective for endemic and non-threatened species was equal to 50% of the geographic range for endemic species with a narrow distribution (area < 1st quartile of the range size distribution) and to 10% for widespread species (area > 3rd quartile of the range size distribution), and it is interpolated log-linearly for all the other species in between. These thresholds were calculated relative to the regional pool of endemic species and log-transformed beforehand. No zone-specific objective was given for exclusively endemic species.

I then modified this area-based objectives on the basis of information about the conservation status of the species such that representation objectives were then increased for threatened species, and further incremented for species both endemic and threatened (n = 7). For this analysis, I defined the objective by interpolating a linear function of the log-transformed range size considering the total pool of species (n=405) and with the following reference points: the first quartile of the range size distribution, below which the representation objective is 100%; and the third quartile of the range size distribution, above which the representation objective is 10%. In addition to this area-based objective definition, I applied a rule on minimum coverage following a decreasing scale: 80% for CR, 50% for EN, and 30% for VU. The final objective was set as the larger value between the minimum coverage values or their linearly interpolated objective. Zone-specific objectives were defined as one third of the overall objective within no-take MPAs.



		Non-threatened	Threatened species		
			VU	EN	CR
Endemic species	Restricted-range	50%	50%	70%	100%
	Intermediate range sizes	linear interpolation			
	Widespread species	10%	40%	60%	100%
No-endemic		Not applied	30%	50%	80%

Figure C6.3 Formulation of conservation objectives for threatened and endemic species. Conservation objectives are shown for each combination of endemic (no-endemic, widespread and restricted-range species) and conservation status ("Vulnerable - VU", "Endangered - EN", "Critically Endangered - CR"). Minimum percentage of coverage are indicated by the inner circles – from 10% for a non-threatened and widespread endemic species to 100%, for CR and endemic with restricted-range species. For this analysis, I defined restricted and widespread species as those having range distribution smaller and larger than the first and third quartile of the range size distribution, respectively. The proportion of the objective required as no-take or multiple-use zones are illustrated by the outer circle (green indicates the coverage required by no-take zones and orange indicates that the remaining objective can be optionally achieved by no-take or multiple-use). Unfilled outer circles indicates that no zone-specific objectives are assigned for endemic and non-threatened species.

For species that are both threatened and endemic, the zone-specific objective was then increased to up to two thirds of the overall objective within no-take MPAs. The most demanding zone-specific objective was assigned to critically endangered species with restricted range (100% of the overall objective within no-take zones).

For connectivity, I identified reef cells containing the top third values (i.e., the upper tercile) for each conservation feature and used their sum to generate my varying conservation objectives (in terms of percentage of total values). For example, reef cells in the top third values for the combination of brooder coral within the northeastern coast (sector) for the out-flux metric made up 90% of the total value across all reef cells; hence, this percentage became the conservation objective (Figure S4).

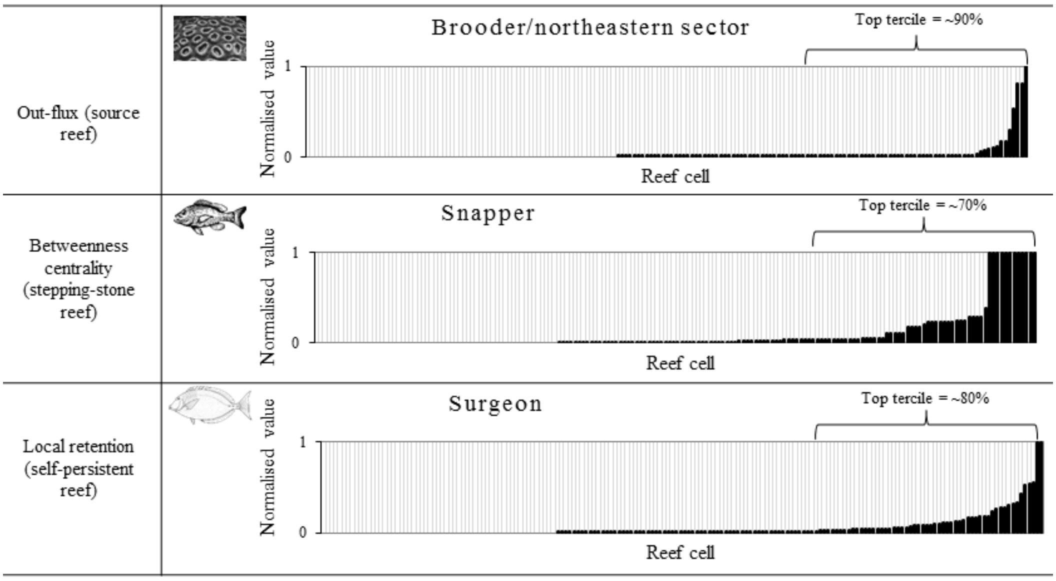


Figure C6.4 Examples of how connectivity objectives were derived. Three connectivity metrics (first column) derived from the biophysical modeling (Magris et al. 2015) for each species (second column) were assigned for each reef cell. Top terciles for each combination of modeled species (brooder, broadcasting coral, snapper, and surgeonfish) and metric (out-flux, betweenness centrality, local retention) were used to estimate the percentage of normalised values to be protected.

Climate warming conservation objectives were set according to the needs and specific management requirements explained in Magris et al. (under review), which consider the historical or future ecosystem state in each regime and are based on the ecological relevance of each regime described in the supporting literature (Figure S5). The suggested MPA type (i.e., no-take or multiple-use) was defined in terms of the historical or future ecosystem state (e.g., areas facing a low level of historical thermal stress are potentially unmodified areas that could still retain a naturally functioning ecosystem and be suitable as no-take areas). The percentage objectives were in turn defined according to the level of ecological relevance present in the rationales from previous studies stating the importance of protecting sites under specific thermal stress regimes. Based on a gradient of ecological relevance, the objectives were set as 100, 50, or 30% of coverage within a specific type of MPA.

Cost in my conservation planning scenarios

The coastal development index was modified from the index originally proposed by Rowlands et al. (2012). The index is measured by the distance from nighttime lights and allowed me to include geographic variability in the cost estimates across the study area included in my prioritization approach. This proxy assumes that reefs situated in close proximity to a source of high-intensity night light are considered less costly to protect than areas situated further away from areas intensely used by humans. The index CDI is based on the metric light proximity index (LPI), as shown in Eq. 1:

$$LPI = \frac{\Sigma L1 \ldots n}{\Sigma D1 \ldots n} \quad (1)$$

where the LPI for a given reef cell is the ratio between L (the recorded intensity of all light sources) and D (calculated as the sum of distances from the centroid of a given reef cell to the centroid of all light sources in the night light imagery). I then calculated the index CDI by rescaling the metric from zero to 1, where a reef cell with a value of 0 has the most intense light source and is associated with the least degree of impediment to management, and a reef cell with a value of 1 is situated furthest away from the light source and is the most costly to manage:

$$CDI = \frac{[(LPI)\times(-1) + (LPI)_{\max} \quad (LPI)_{\min}]}{(LPI)_{\max}} \quad (2)$$

where LPI is the LPI calculated for a given reef cell, and $(LPI)_{\max}$ is the maximum value registered for any cell in the study region. I included the CDI values as a measure of the relative cost for each reef cell in my Marxan analyses (see below).

Conservation planning settings

I used the Marxan with Zones conservation planning software (Watts et al., 2009) to create an expanded MPA and clean slate scenario. For the expanded MPA scenario, reef cells were considered protected if they overlapped with MPAs by more than 50%. The boundary length modifier and the zone boundary cost were optimized for each set of objectives according to Stewart and Possingham (2005) and Watts et al. (2008). All MPA design scenarios presented here were repeated 100 times (10 million iterations for each run) (Ball & Possingham, 2000).

Management cost evaluation

I performed a linear regression analysis of previously published management costs for predicting the total management cost of MPAs based on the size of the proposed protected area because of the known and well-established relationship between the ratio costs per unit area and the total amount of area to be protected: the per-unit-area costs decrease with the total MPA area (Balmford et al., 2004; Ban et al., 2011). This relationship represents one of the best drivers associated with financial resources for conservation (Gravestock et al., 2008).

I used budget information related to staff expenses, operational costs (such as enforcement and monitoring activities), and infrastructure from existing no-take and multiple-use MPAs in Brazil ($n = 10$) to empirically fit the model. A linear regression model was used to determine the relationship between the annual management cost per km^2 and the area in km^2. The values for fitting the model were based on the budgetary information for each management plan for both types of MPAs. I extracted this information from management plans available at www.icmbio.gov.br. Data were standardized in relation to the budget time frame and were converted into US dollars at 2015 exchange rates after applying the average inflation rate from the time of the plan publication to 2015. On average, I found that no-take MPAs were 2.3 times more costly than multiple-use ones. Because I used data for management plans for existing MPAs situated outside my study area, I had to assume that type of ecosystem protected and geographic variability had no interference in management cost predictions. The adjusted coefficient of determination was used to assess the regression model performance.

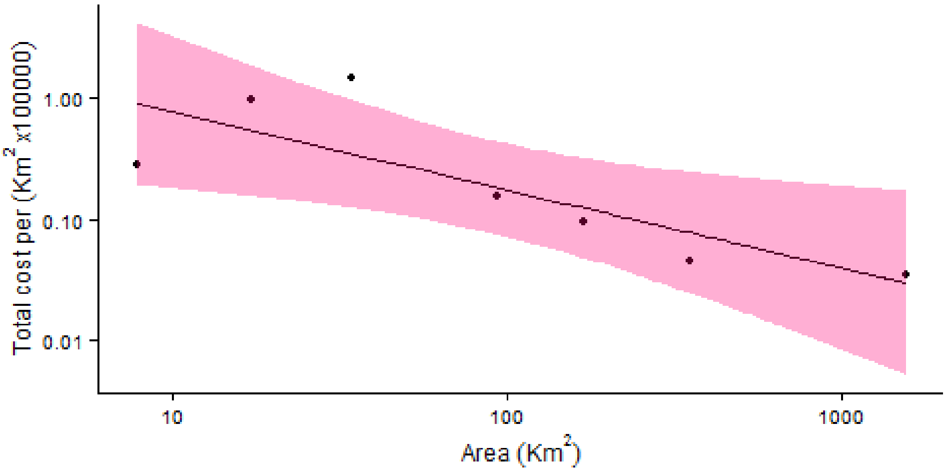


Figure C6.5 Regression model of management cost predicted based on area to be protected by No-take MPAs. Dots represent data from existing MPAs and contour indicates 95% confidence bounds for the prediction mean line.

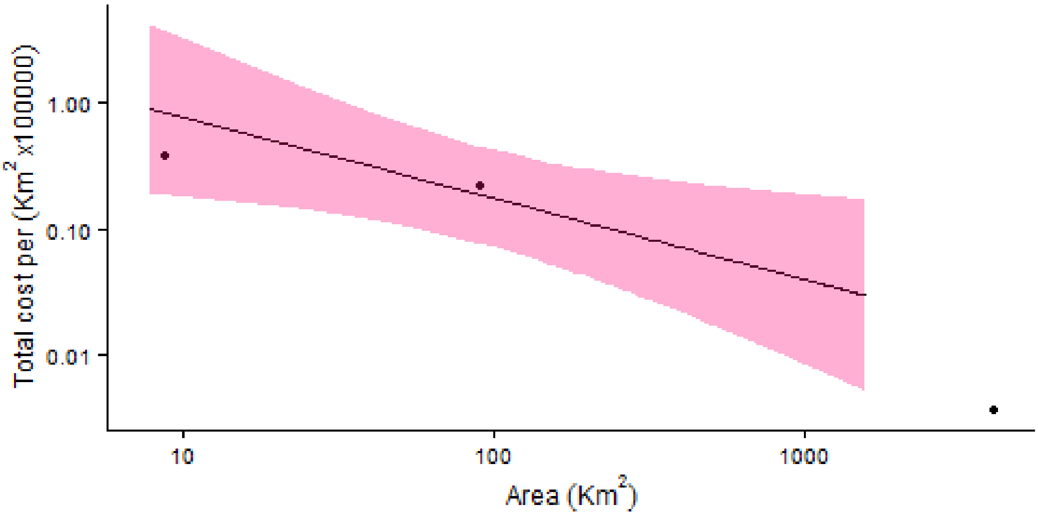


Figure C6.6 Regression model of management cost predicted based on area to be protected by multiple-use MPAs. Dots represent data from existing MPAs and contour indicates 95% confidence bounds for the prediction mean line

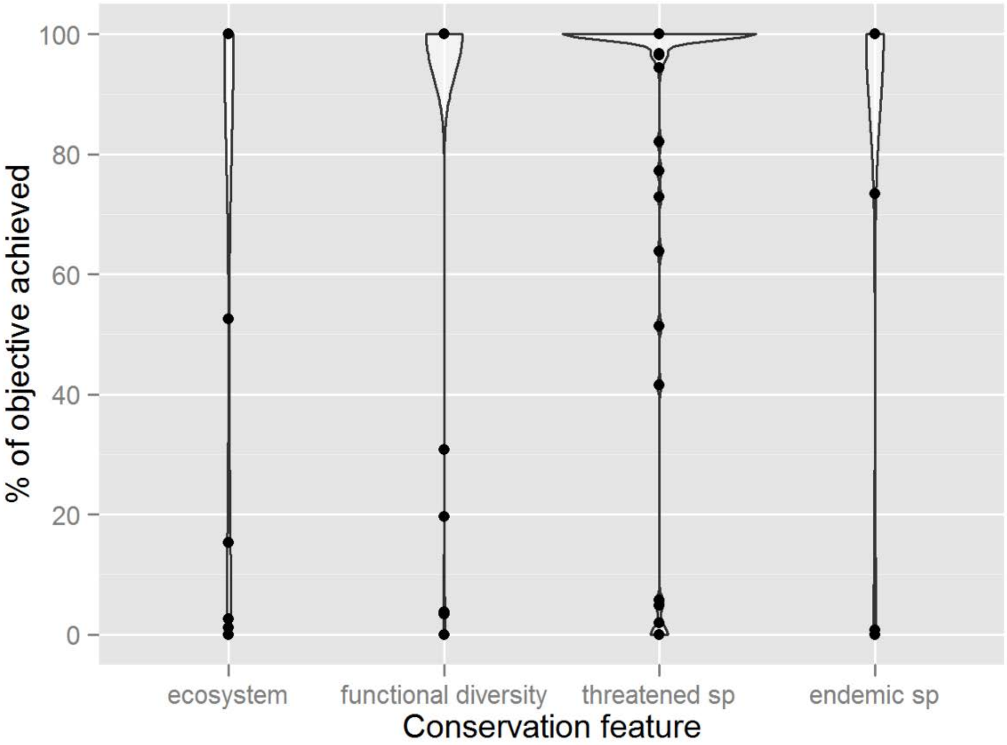


Figure C6.7 Results for objective achievement stratified by the type of conservation feature for biodiversity.

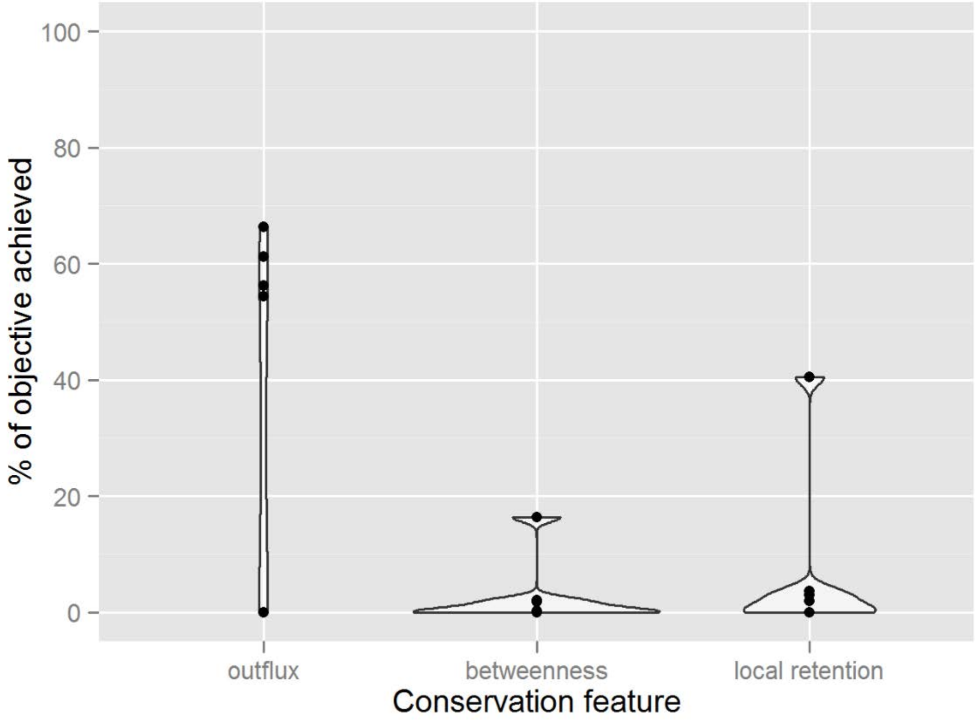


Figure C6.8 Results for objective achievement stratified by the type of conservation feature for connectivity.

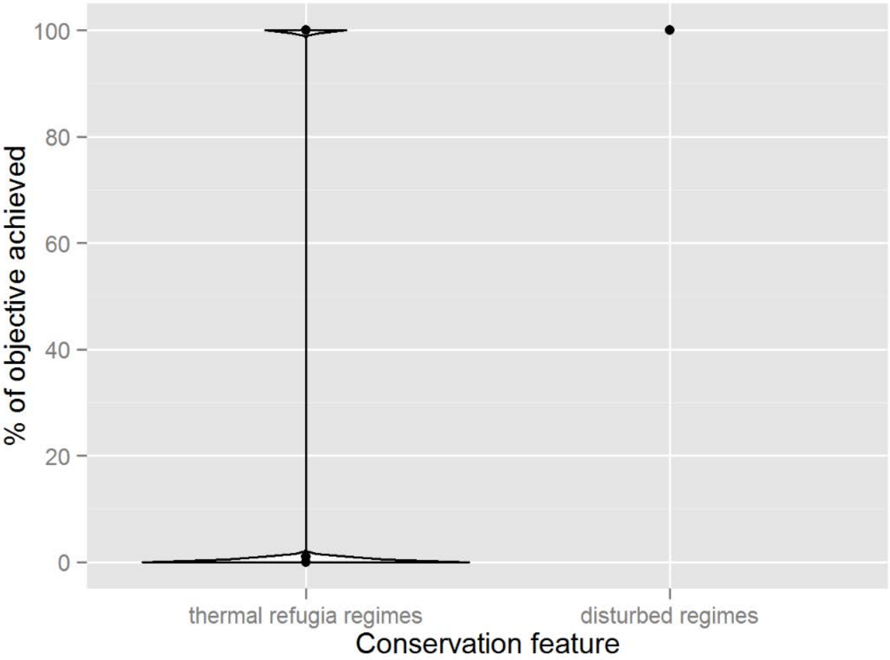


Figure C6.9 Results for objective achievement stratified by the type of conservation feature for climate warming.