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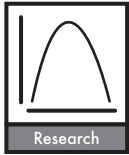


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Integrating multiple species connectivity and habitat quality into conservation planning for coral reefs

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Incorporating connectivity into the design of marine protected areas (MPAs) has met with conceptual, theoretical, and practical challenges, which include: 1) the need to consider connectivity for multiple species with different dispersal abilities, and 2) the role played by variable habitat quality in determining the spatial patterns of connectivity. We propose an innovative approach, combining biophysical modeling with a routinely-used tool for marine-reserve design (Marxan), to address both challenges by using ecologically-informed connectivity parameters. We 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 modeled species and, also across species, we 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. We also found that caution is needed in combining connectivity data from modeled species into multi-species matrices, which do not perform reliably as surrogates for all connectivity metrics of individual species. We then showed that restricting the habitat available for conservation has an inequitable impact on different connectivity objectives and species, with greatest impact on betweenness centrality and long-distance dispersers. We used Brazilian coral reefs as a case study but our 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.

Systematic conservation planning (Margules and Pressey 2000) has been widely recognized 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 (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 (Roberts et al. 2003, Palumbi 2004, Sale et al. 2005, Botsford et al. 2009, Cowen and Sponaugle 2009). 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 impacts will rely largely upon species’ dispersal ability (Hughes et al. 2005, Jones et al. 2007, Almany et al. 2009). 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 marine protected areas (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 (Planes et al. 2009, Harrison et al. 2012, Olds et al. 2012). 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. 2010, 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 modeling can provide powerful insights into larval connectivity and the required designs of MPA networks (Cowen et al. 2003, Sale et al. 2005, Treml et al. 2008, White et al. 2010a, Treml and Halpin 2012), 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. 2010a).

While biophysical modeling 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 (Cowen et al. 2006, Beger et al. 2010, 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, we extend previous approaches to MPA network design that consider connectivity by simultaneously integrating multiple species connectivity and local habitat quality. We 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 modeling and remote sensing. Our approach improves integration of connectivity in four ways. First, we 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, we 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, we test how well planning for connectivity of multiple species achieves connectivity for individual species. Lastly, we explore the relationship between maintaining highly-connected MPAs and the total area available for conservation.

Methods

Brazilian reefs

We used Brazilian coral reefs as a case study. While our study region is considered a conservation priority in the southwestern Atlantic Ocean (Leão and Dominguez 2000), coral reefs in Brazil are also faced with intensifying threats from local and global pressures (Barreira e Castro et al. 2012). Direct and indirect stressors include overfishing and destructive fishing techniques (Pinheiro et al. 2010, Freitas et al. 2011), coastal development and associated runoff of terrestrial sediment (Segal and Castro 2011, Barreira e Castro et al. 2012), and disturbances related to climate change (Leão et al. 2010, 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.

Biophysical modeling procedures

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

Habitat data

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 2000 reef locations (approximate area of 889 km²). Because our 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 × 10 km). The rescaling resulted in a grid-based model with 176 reef cells (Fig. 2A, upper left of Fig. 3), each attributed with a proportion of reef extent.

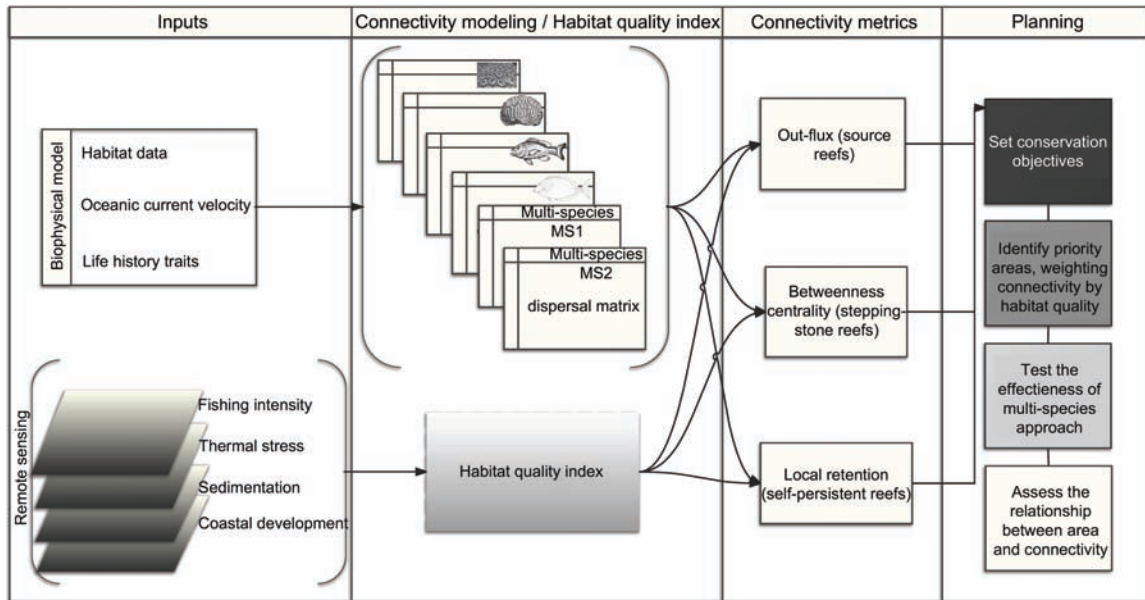


Figure 1. Major steps in developing our approach to integrate connectivity into conservation planning. Inputs for biophysical modeling and stressors were used to produce dispersal matrices for four candidate species and a composite index for habitat quality, respectively. Matrices for the four species 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.

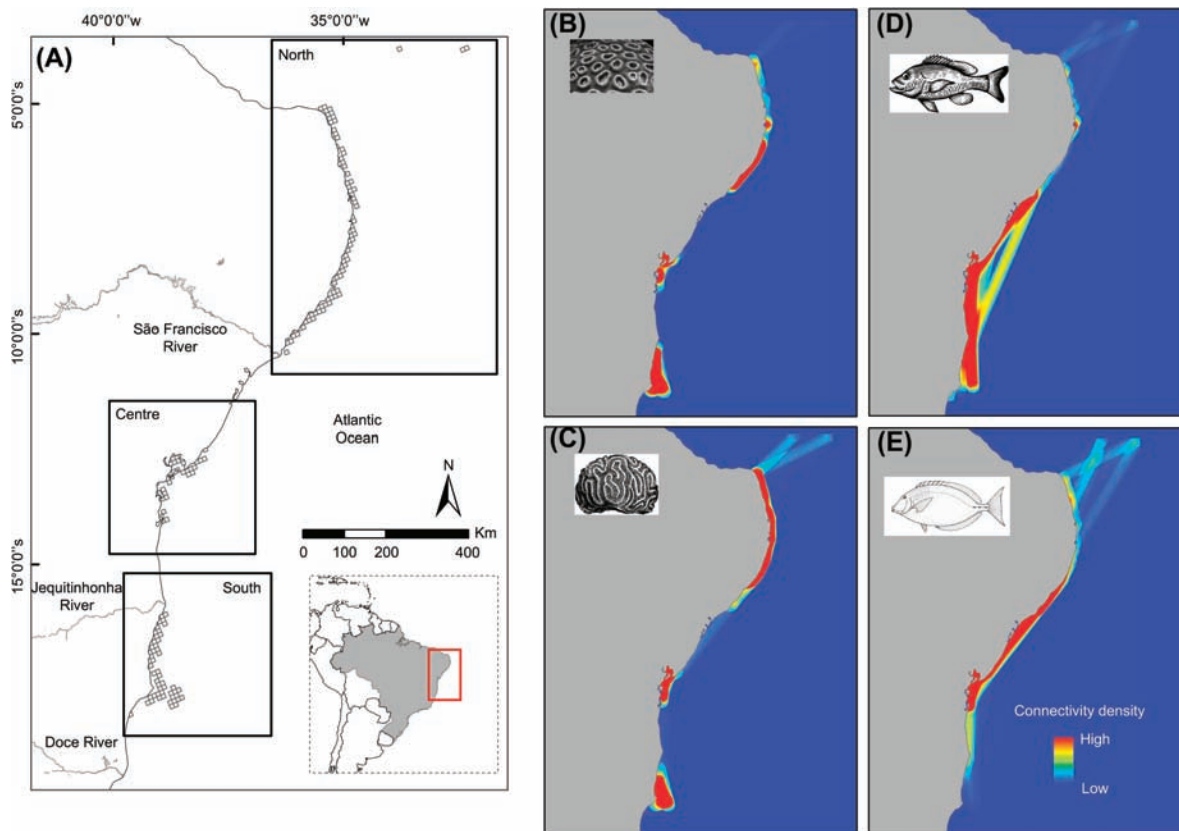


Figure 2. (A) The study region encompasses the northeastern and eastern coast of Brazil (southwestern Atlantic). 176 reef cells were grouped into three sectors (north, centre, and south) to facilitate geographic description. (B) Connectivity density among reef cells for the brooder coral. Only demographically-strong 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.

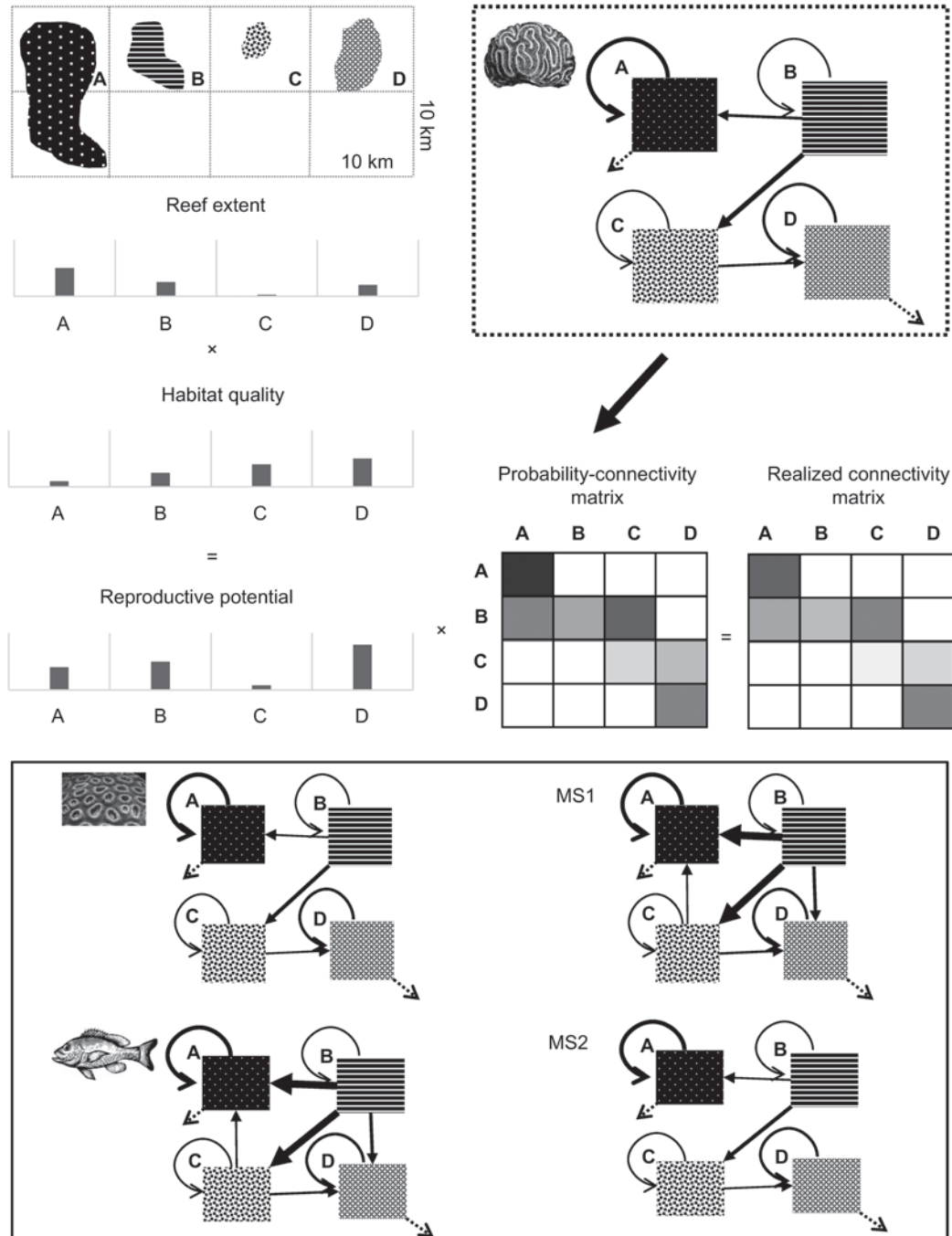


Figure 3. Integration of habitat quality in our connectivity models. Raw data on reef locations contained in our grid-based habitat map (10×10 km spatial resolution) were defined as reef cells (A–D, upper left), each attributed with proportional reef extent, habitat quality, and reproductive potential. In the upper right, connectivity networks, illustrated for the broadcast coral, were derived from the biophysical modeling, 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 realized connectivity matrix for each species, used to calculate all connectivity metrics. We 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, we 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 modeling system based on the eddy-resolving $1/12^\circ$ 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

Table 1. Biological parameters used in the biophysical modeling 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

winds, rivers, tides, radiation, and precipitation fluxes over the entire domain. More information on Atlantic RTOFS is available at: < www.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 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 (Pires et al. 1999, 2011, Neves and Pires 2002, Rocha et al. 2002, Neves and Silveira 2003, Lins-de-Barros and Pires 2007, Freitas 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.

Connectivity modeling

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. 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. We 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. Our simulations modeled 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. We used this

information to build an asymmetric connectivity-probability matrix (centre-right of Fig. 3).

The connectivity strength between every pair of reef cells was defined as the probability of settling in a destination reef j from a source reef i (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, we 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 (Table 1) (Treml et al. 2012). We 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).

We merged the connectivity data for the four modeled species to produce multi-species matrices, using two methods (bottom of Fig. 3). First, we used the probability of at least one connection between each pair of reef cells in any species (MS1, see Eq. 1, below). We termed this approach 'inclusive' because it included all sites important for the connectivity of any one species. This approach maximized the network size (i.e. total number of connections within the network). In the second approach, we considered each pair of reef cells to be connected only if they were connected for all four species (MS2, see Eq. 2, below). We 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 we were 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, we generated models that we 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:

$$p_{ij}^{MS1} = 1 - \left[(1 - p_{ij}^{BO}) \times (1 - p_{ij}^{BR}) \times (1 - p_{ij}^{SN}) \times (1 - p_{ij}^{SU}) \right] \quad (1)$$

where p_{ij}^{MS1} is the probability of dispersal between cells i and j for the multi-species matrix in the MS1 approach, p_{ij}^{BO} is the probability of dispersal between cells i and 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:

$$P_{ij}^{MS2} = P_{ij}^{\min} \quad (2)$$

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

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

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. 1, Table 2), all known to have significant impacts on coral cover or fish abundance (Bellwood et al. 2004, Mouillot et al. 2013). Our aim was not to produce an accurate predictor of ecological responses to anthropogenic 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 characterized by substantial losses of coral cover, proliferation of macroalgae, and marked reductions in fish biomass (Hughes 1994, Dinsdale et al. 2008).

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 our 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, we collected spatial data relating to the annual maximum DHWs for each coral reef cell.

Table 2. Details of stressors that were used for developing the habitat quality model. For more information, see the Supplementary material Appendix 1.

Index	Data source	Method	Equation	Definitions
Fishing intensity	Google Earth Pro and government reports	Linear decay model for both artisanal and industrial fishery pressures	$F_T = \sum_{i=1}^{426} f d_{Ti} \times (P_{Ti} \times B_T)$ $= Z_i \left(\sum_{i=1}^{17} f d_{Ti} \times (P_{Ti} \times B_i \times E_i) \right)$	F_T and F_i are the potential impact of traditional and industrial fisheries, respectively; $f d_{Ti}$ is a distance decay factor $(0 - 1)$ derived from the minimum at sea distance from the centroid of a reef cell to the i^{th} port; P_{Ti} is the number of traditional vessels in the i^{th} port; B_T is the difference in visual sampling efficiency of the traditional sector; Z_i – the likely fishing use of a cell based on the depth of the cell – is set equal to 1; f d_{Ti} , P_{Ti} , B_T are the decay factor, number of vessels, and correction factor, respectively; and E_i represents the efficiency of industrial vessels relative to traditional vessels 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
Thermal stress	NOAA AVHRR sensor series	Degree Heating Weeks (DHW)	$DHW = \sum_{i=1}^{n_w} x_{w,i}$ $x_w = \begin{cases} T_H - T_M & \text{when } x_w > 1.0 \\ 1.0 & \text{otherwise} \end{cases}$	The value of K490 represents the rate at which light intensity at 490 nm is attenuated with depth
Sedimentation	MODIS Aqua	Diffuse attenuation coefficient at 490 nm (K490)	$WCI_K = K490$	
Coastal development	DMSP/NOAA/NGDC nighttime satellite imagery	Light proximity index LPI	$LPI = \sum \frac{L_1 \dots L_n}{D_1 \dots D_n}$	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

We 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 and Atmospheric Administration, National Geophysical Data Center (NOAA/NGDC). More details on the calculation of the proxy measures of stressors are in Supplementary material Appendix 1.

Habitat quality index

We 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. 1). Each factor individually, as well as the composite index, was normalized to the reference range of zero to one (zero indicating poorest-quality habitat and 1 representing best-quality habitat), as follows:

$$HQI = \frac{(RFI + TSI + WCI + CDI) - (RFI + TSI + WCI + CDI)_{\min}}{(RFI + TSI + WCI + CDI)_{\max} - (RFI + TSI + WCI + CDI)_{\min}} \quad (3)$$

where HQI is the index of relative habitat quality, RFI is the fishing-intensity index, TSI is the thermal-stress index, WCI is the sedimentation (water-clarity) index, and CDI is the coastal-development index. The subscripts min and max of Eq. 3 indicate the minimum and maximum overall score, respectively, of any reef cell across the study region. Our modeling 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.

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. 1). Out-flux is related to the source-strength of a patch (a reef cell in our 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 (Minor and Urban 2007, Figueira 2009). 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 (Urban and Keitt 2001, Minor and Urban 2007, Treml et al. 2008). 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 (Figueira 2009, Burgess et al. 2014).

Probability matrices from all four candidate species and the two multiple-species approaches were converted to realized dispersal matrices by calculating larval flux between patches, adapting the formulae of Urban and Keitt (2001) (see centre of Fig. 3):

$$f_{ij} = RPO_i \times p_{ij} \quad (4)$$

$$RPO_i = \frac{s_i}{s_{\text{tot}}} \times HQI_i \quad (5)$$

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 relativized 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). We 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 realized matrices, then counting the number of times those paths crossed each patch (Minor and Urban 2007). We measured local retention for each cell as the diagonal elements of realized dispersal matrices (Treml et al. 2012).

Planning for connectivity

We sought to optimize total connectivity benefits of a network of notional protected areas by considering all the connectivity metrics described here. We 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. 1). We 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 our analyses, we 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, we also recorded the cost as equal to the reef area.

To select priority areas (Fig. 1), we specified the quantities at which conservation features (combinations of metrics and candidate species) should be represented in the MPA network. We 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 our conservation objective. Across all features, objectives varied from 45 to 67% of total values. Consequently, our approach simultaneously prioritized 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, we created 100 solutions to identify the set of planning units that met our 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, we 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. We 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 our 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, we 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, we 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, we 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, we 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. We tested for differences with one-way ANOVA followed by Tukey's post-hoc test.

Finally, we 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 we 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.

Dataset and analysis caveats

Ideally, including more direct measures of reef quality (e.g. coral cover or fish biomass) within our 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 standardized field

data over such a large area was beyond our available resources. Instead, our 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 (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). Our principal concern was the potential effect of habitat quality, assessed with plausible spatial variables, on modeled connectivity and prioritization outcomes.

A significant consideration in planning is temporal explicitness of data. We were unable to address temporal dynamics associated with our stress factors and connectivity metrics. Our proxies for habitat quality are likely to change over time, and our 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 our habitat quality index we also excluded potential interactions between threats and had to aggregate the variables considering different timeframes. Although our 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 we used in our modelling can reflect the impact of widespread anthropogenic influences, our stressors are likely to interact differently in different parts of the study region, making predictions of ecological responses uncertain.

Results

Inter-specific differences in dispersal ability were clearly visible (Fig. 2B–E). By assessing demographically-relevant connections for the brooder species we were able to identify three major assemblages of reef cells ('sectors') with connections within but not between sectors (Fig. 2B): 1) coastal banks off the northeastern coast – termed 'north' sector in Fig. 2A, 2) a mixture of fringing reefs and banks in northern Bahia State – 'centre' sector in Fig. 2A, and 3) a southern Bahia area with coastal and outer arcs of reefs in the Abrolhos region – 'south' sector in Fig. 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. 2C). For the snapper, connectivity between the central and south sectors was particularly strong (Fig. 2D). The surgeonfish was also generally well-connected across the study region, and particularly in the north and central sectors (Fig. 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 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 our study region (Fig. 4A and B). However, incorporating habitat quality into biophysical models reduced the potential reproductive output throughout study area (Fig. 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, our 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).

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. 5). Some similar spatial patterns of connectivity metrics were apparent across species (Fig. 5, Fig. 6 and Supplementary material Appendix 1–2). 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. Cabralia 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, we found that spatial priorities changed when we progressively incremented the number of species considered (Supplementary material Appendix 2, Fig. A5).

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

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). We also found that imposing the cost constraint of scenario 2 had uneven effects on connectivity across species and

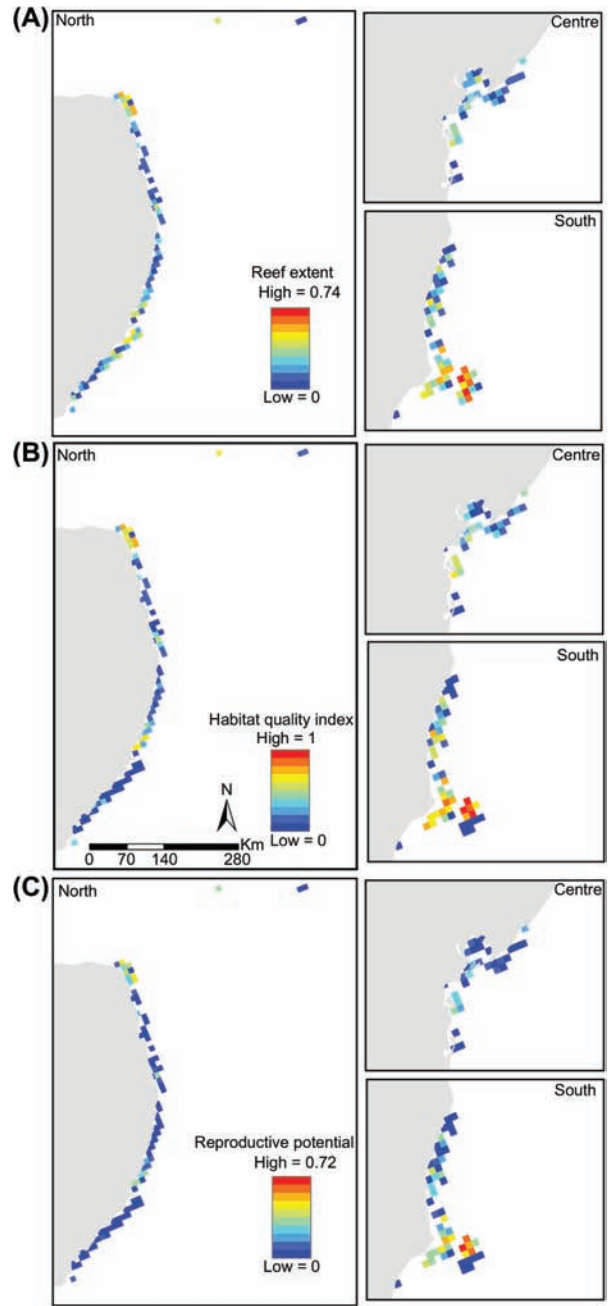


Figure 4. Influence of habitat quality. Values for extent of reefs (A), habitat quality index (B), and extent weighted by habitat quality (reproductive potential) (C) in reef cells. Our spatial model of habitat quality produced a spatially-heterogeneous composite index that indicated the combined exposure of reef cells to fishing pressure, thermal stress, sedimentation, and coastal development.

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 3 and Supplementary material Appendix 2). Both multi-species methods performed reasonably well for out-flux, with no

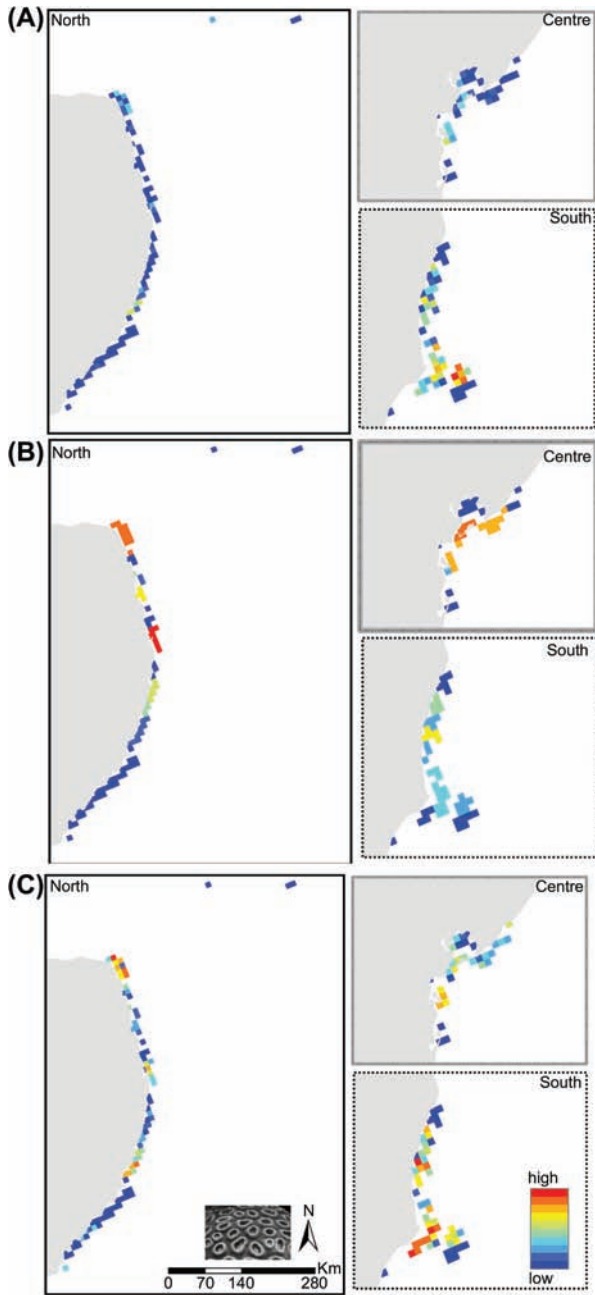


Figure 5. Spatial distribution of connectivity metrics for the brooder coral in Brazil: (A) out-flux, (B) betweenness centrality, and (C) local retention. See Supplementary material Appendix 2, Fig. A3 and A4 for corresponding data on the broadcasting coral and the snapper.

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.

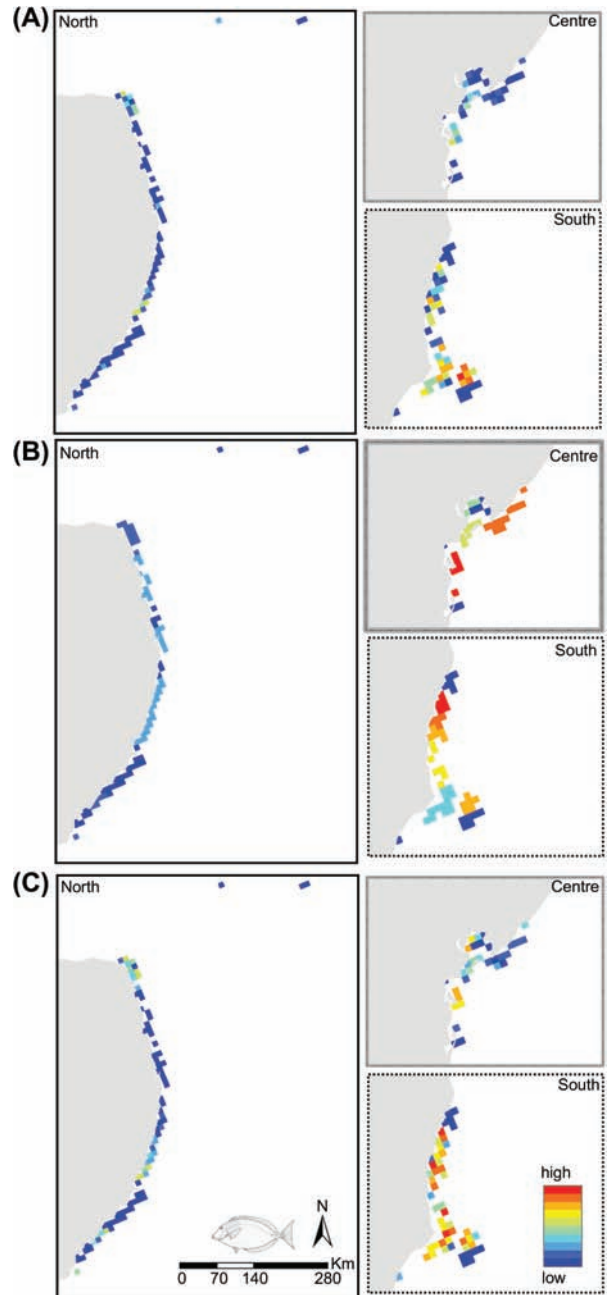


Figure 6. Spatial distribution of connectivity metrics for the surgeonfish in Brazil: (A) out-flux, (B) betweenness centrality, and (C) local retention. See Supplementary material Appendix 2, Fig. A3 and A4 for corresponding data on the broadcasting coral and the snapper.

Restricting to 10% the total reef area available for achieving our conservation objectives markedly affected the overall connectivity value of our notional MPA network, with the greatest impacts on betweenness centrality and local retention (Fig. 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

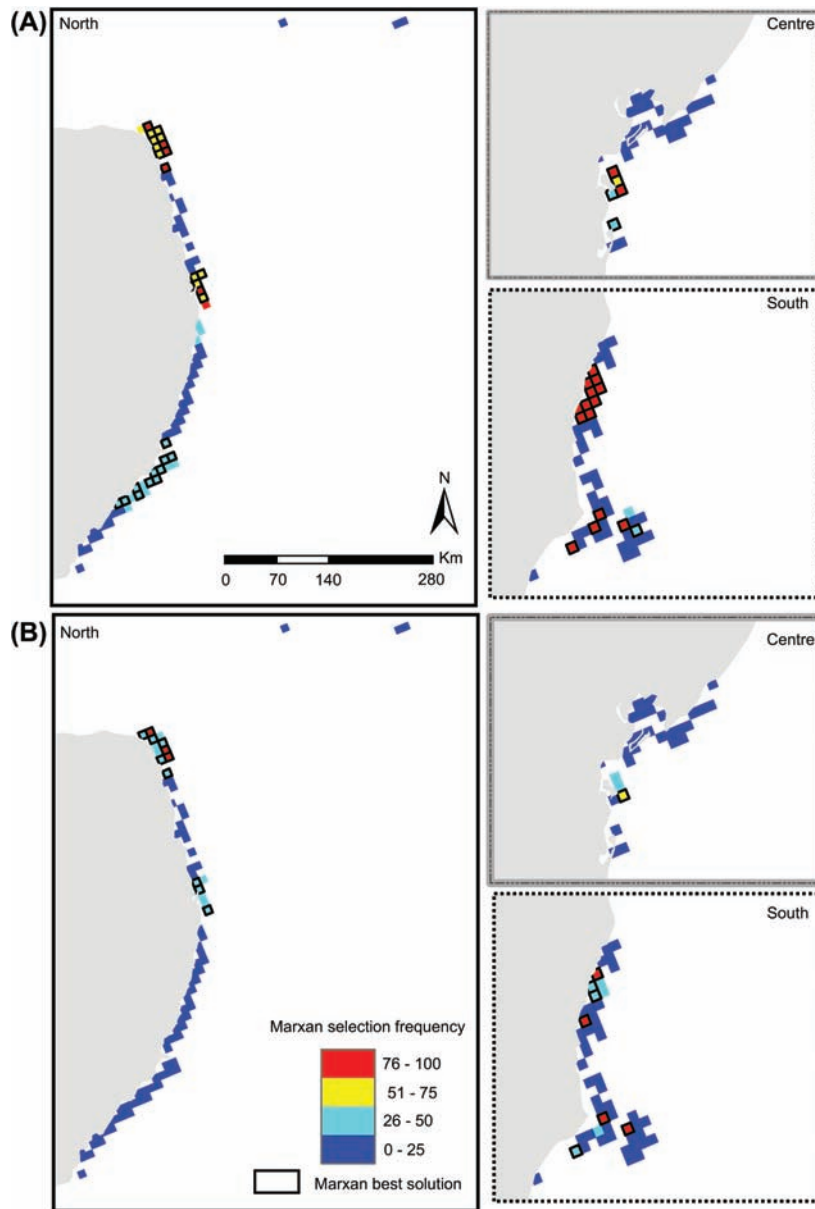


Figure 7. Selection frequencies and best-solution outputs from Marxan. Conservation objectives are based on top-tercile values for each conservation (connectivity) feature with no restriction in terms of coverage (A) and constrained by a maximum cost (10% of total extension of reefs, (B)).

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.

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). Our 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. Our results emphasize that information on habitat quality can substantially alter modelled dispersal patterns. We 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'

Table 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 Supplementary material Appendix 2.

		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	✗	✓

dispersal abilities (Magris et al. 2014). Recent applications have developed methods for quantitatively addressing connectivity in relation to spatial dependencies between conservation features (Edwards et al. 2009, Begger et al. 2010, Jacobi and Jonsson 2011, Lehtomäki and Moilanen 2013, White et al. 2014). Our study builds upon this previous work in several ways. Firstly, we 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, we 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, we 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). Our approach demonstrates one way of improving the ecological basis of designing MPA networks by increasing the chances of maintaining functional demographic connectivity.

We applied our 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 km² spatial resolution. We used biophysical modeling coupled with Marxan to find MPA configurations guided by connectivity-based metrics. Nevertheless, our 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. Our 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).

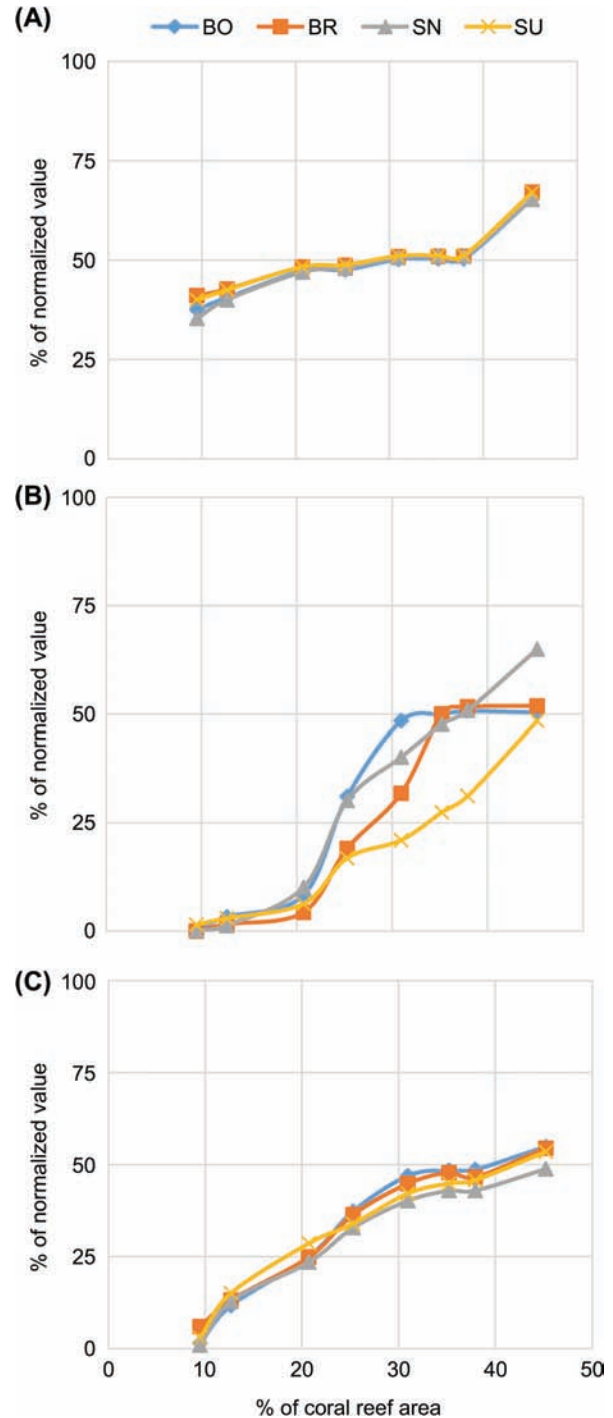


Figure 8. Relationship between connectivity, as measured by out-flux (A), betweenness centrality (B), and (C) local retention, and the total reef area selected for conservation. The curves show the percentage of normalized connectivity values for each of the four species: BO denotes the brooder coral, 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.

The relevance of different life history traits

Our 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. We 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. Our 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.

Our 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 our 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 our results can be generalized across other taxa. Further research could also explore how uncertainty around biological parameters used for modeling connectivity influence the selection of places for protection.

Habitat-quality index and connectivity metrics

By investigating the influence of both habitat availability and quality in the number of larvae released, we extended the scope of a previous study by Trembl et al. (2012), who determined predictors of broad-scale connectivity in marine populations when quantifying the geographic structure of the dispersal kernel. In our 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. Our 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. Our 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 our stressors predicts reef health. For now, though, the use of proxies such as ours 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).

We identified new opportunities for conserving coral-reef ecosystems in the South Atlantic Ocean in the Abrolhos Bank, the Cape of São Roque, the Cabralia reefs, Itacolomis, and between Camamu and Tinhaí. 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 (Leão 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, we 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 the Supplementary material Appendix 2, Fig. A5). 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 we 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 analyzing the connectedness of potential MPA networks. One way forward is to measure the relative influence of metrics on demographic persistence using metapopulation modeling, which provides insights into balancing the amount of habitat and potential connectivity (Watson et al. 2011b).

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 (White et al. 2010b, Jacobi and Jonsson 2011, Andreollo et al. 2015). 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 (Trembl and Halpin 2012), ours is the first study to determine whether combined connectivity matrices are effective as surrogates for individual species. We 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.

We 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. Our results on the surrogacy

value of multi-species matrices were variable, so we could not draw general conclusions about their likelihood of catering for all metrics across species with a variety of dispersal patterns. While we 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). We 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).

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 (Beger et al. 2009, Edwards et al. 2009). Other recent advances have also indicated ways forward. Andreello 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 socioeconomics 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 our methodological template to deal with tradeoffs and alignments of objectives in a multi-criteria optimization problem (Wilson et al. 2009), our 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, we showed that it would be possible to use hypothetical species for sensibly guiding conserva-

tion decisions without a thorough knowledge of species' life histories in data-poor regions.

Our 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. 2010), and design based on single connectivity metrics (White et al. 2014). Although we acknowledge recent attempts to select optimum networks of MPAs based on connectivity (Jacobi and Jonsson 2011, Berglund et al. 2012, Andreello et al. 2015), the contribution of our study is to incorporate species with contrasting connectivity abilities and habitat quality into conservation planning tools with the assistance of biophysical modeling and remote sensing. We 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, we hope that this study might bring connectivity and persistence into ongoing efforts to expand the network of MPAs off the Brazilian coast.

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Supplementary material (Appendix ECOG-01507 at <www.ecogeography.org/readers/appendix>). Appendix 1–2.