

Prioritising seascape connectivity in conservation using network analysis

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Summary

1. Connectivity is regarded globally as a guiding principle for conservation planning, but due to difficulties in quantifying connectivity, empirical data remain scarce. Lack of meaningful connectivity metrics is likely leading to inadequate representation of important biological connections in reserve networks. Identifying patterns in landscape connectivity can, theoretically, improve the design of conservation areas.

2. We used a network model to estimate seascape connectivity for coral reef-associated fishes in a subtropical bay in Australia. The model accounted for two scales of connectivity: (i) within mosaics at a local scale and (ii) among these mosaics at a regional scale. Connections among mosaics were modelled using estimations of post-larval small and intermediate movement distances represented by home ranges of two fish species.

3. Modelled connectivity patterns were assessed with existing data on fish diversity. For fishes with intermediate home ranges (0–6 km), connectivity [quantified by the index Probability of Connectivity (*dPC*)] explained 51–60% of species diversity. At smaller home ranges (0–1 km), species diversity was associated closely with intramosaic connectivity quantified by the index *dPC*_{intra}.

4. Mosaics and their region-wide connections were ranked for their contribution to overall seascape connectivity and compared against current positions and boundaries of reserves. Our matching shows that only three of the 10 most important mosaics are at least partly encompassed within a reserve, and only a single important regional connection lies within a reserve.

5. *Synthesis and applications.* Notwithstanding its formal recognition in reserve planning, connectivity is rarely accounted for in practice, mainly because suitable metrics of connectivity are not available in planning phases. Here, we show how a network analysis can be effectively used in conservation planning by identifying biological connectivity inside and outside present reserve networks. Our results demonstrate clearly that connectivity is insufficiently represented within a reserve network. We also provide evidence of key pathways in need of protection to avoid nullifying the benefits of protecting key reefs. The guiding principle of protecting connections among habitats can be achieved more effectively in future, by formally incorporating our findings into the decision framework.

Key-words: connectivity, conservation planning, coral reef, fish movement, marine conservation, marine reserves, network model, seascape

Introduction

Connectivity is a key determinant of ecosystem functioning (Levin & Lubchenco 2008). It occurs through

exchanges of nutrients, matter and organisms and plays a critical role in regulating ecological processes (Bauer & Hoye 2014). It is believed that increased connectivity enhances resilience of metapopulations by linking subpopulations between distinct habitats (McClanahan *et al.* 2012; Saura *et al.* 2014). The importance of quantifying multiscale and multipurpose connectivity has become

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increasingly clear in the face of biodiversity loss and climate change (Rayfield *et al.* 2016).

Connectivity is now viewed as a critical criterion for successful conservation (Foley *et al.* 2010; Krosby *et al.* 2010; Liqueste *et al.* 2015); however, the multiple scales of linkages among populations and ecosystems complicate its incorporation into spatial planning (Beger *et al.* 2010; Minor & Lookingbill 2010). Despite being explicitly formulated as a guiding principle, quantitative data on the conservation value of connectivity are rarely available (NRC 2001; Pendoley *et al.* 2014; Olds *et al.* 2016). It is widely accepted that individual reserves should be part of larger connected conservation networks, but estimations of connectedness are often based on single-area metrics instead of network metrics, which incorporate linkages among multiple areas (Wedding *et al.* 2011; Magris *et al.* 2014).

Movements of larval, juvenile and adult fishes maintain connectivity among ecosystems in the marine environment (Hamilton *et al.* 2012; Huijbers *et al.* 2013; Welsh & Bellwood 2014). These movements include larval dispersal and daily activities by post-larval fish, such as foraging and seeking shelter, as well as potentially larger scale ontogenetic and spawning migrations (Green *et al.* 2015). Fish thus depend on, but also create, connectivity, acting as mobile links that contribute to ecosystem processes. Factors such as distance and habitat type, which determine risk and movement cost, influence movement behaviour (Sheaves 1993; Turgeon *et al.* 2010). In functional terms, this means that fish movements link different habitats and form diverse habitat networks in seascapes (Mumby & Hastings 2007; Wiens 2009). Incorporating this seascape connectivity into conservation planning requires analytical tools that address the complexity of networks and the connections they contain.

Network analysis is a branch of mathematics used to examine connectivity in real-world systems (Urban *et al.* 2009; Rayfield, Fortin & Fall 2011). In ecology, network analysis is increasingly used to identify the role of habitat units in landscapes, such as stepping stones and key connections for animal movement (Stewart-Koster, Olden & Johnson 2015; Rayfield *et al.* 2016), and help to prioritise areas for conservation (Gurrutxaga, Rubio & Saura 2011; Saunders *et al.* 2016). These approaches can explicitly identify important areas for landscape connectivity over both short and long temporal scale (Rayfield *et al.* 2016) and identify locations for management interventions at local and landscape scales given probable species movements (Minor & Lookingbill 2010; Stewart-Koster, Olden & Johnson 2015).

Currently, most of these studies examine connectivity through animal movement in terrestrial ecosystems (e.g. Minor & Lookingbill 2010; Saura *et al.* 2014). In the aquatic environment, passive larval dispersal is a major driver of population dynamics and the majority of studies, including those using network analysis, focus on estimating this form of connectivity (Trembl *et al.* 2008; Beger *et al.* 2010). Multispecies larval dispersal has also been modelled in combination with social connectivity using

network analysis (Trembl *et al.* 2015). Nevertheless, the movement of adult species is important for many ecosystem processes, including reproduction (Mumby & Hastings 2007; Green *et al.* 2015). Network analysis has been used to describe the spatial dynamics of post-larval fish movement as an indicator for ecosystem vulnerability (Fox & Bellwood 2014) and to examine habitat usage (Finn *et al.* 2014; Lédée *et al.* 2015).

Previous theoretical studies identified the specific value of network indices for connectivity analysis and habitat conservation (Saura & Rubio 2010; Baranyi *et al.* 2011; Rayfield, Fortin & Fall 2011). We apply these indices to quantify the probable connectivity of a regional marine ecosystem including multiple habitat types and multiple fish species with different movement scales.

Here, we demonstrate the potential for network analysis to provide baseline information on multiscale connectivity for fish movement and prioritise its integration in marine spatial planning. We used a network model to analyse spatial relationships in a seascape, including local-scale connectivity within mosaics and regional-scale connectivity among mosaics in the network. We used data on fish diversity to assess how well connectivity patterns created by the model fitted an ecological pattern. The model was used to evaluate the extent to which existing marine reserves incorporate key seascape connections for coral reef-associated fishes and allows us to provide guidance on modifications to the reserve network to improve conservation outcomes.

Materials and methods

In this study, we modelled connectivity within and among habitat mosaics for post-larval fish in a subtropical embayment (Fig. 1). The spatial and temporal scale to which our study applies is the 'home range' scale, which is defined as the area in which routine (e.g. daily) movements, such as foraging and seeking, occur (van Dyck & Baguette 2005; Green *et al.* 2015). The review by Green *et al.* (2015) indicated that approximately 40% of the 145 studied reef and coastal pelagic fish species show linear home range movements between 0.5 and 10 km. To account for the different movement capacities present in a multispecies assemblage, we selected two different fish species to represent different home ranges and modelled connectivity over a range of different potential movement thresholds (Fig. 2). Seascape connectivity was estimated with a proximity index and the graph theory-based index *Probability of Connectivity (PC)*. To calculate the *PC* index, connectivity in the bay was modelled as a spatial network. The model estimated probabilities of connectivity according to specified threshold distances that represented maximum home range movements (Saura & Pascual-Hortal 2007).

STUDY AREA

The research area was Moreton Bay, a large subtropical embayment in eastern Australia that includes a network of no-take reserves managed as part of the Moreton Bay Marine Park. Reserve boundaries in the park were revised in 2008 based on nine biophysical and four socio-economic guiding principles (NRC

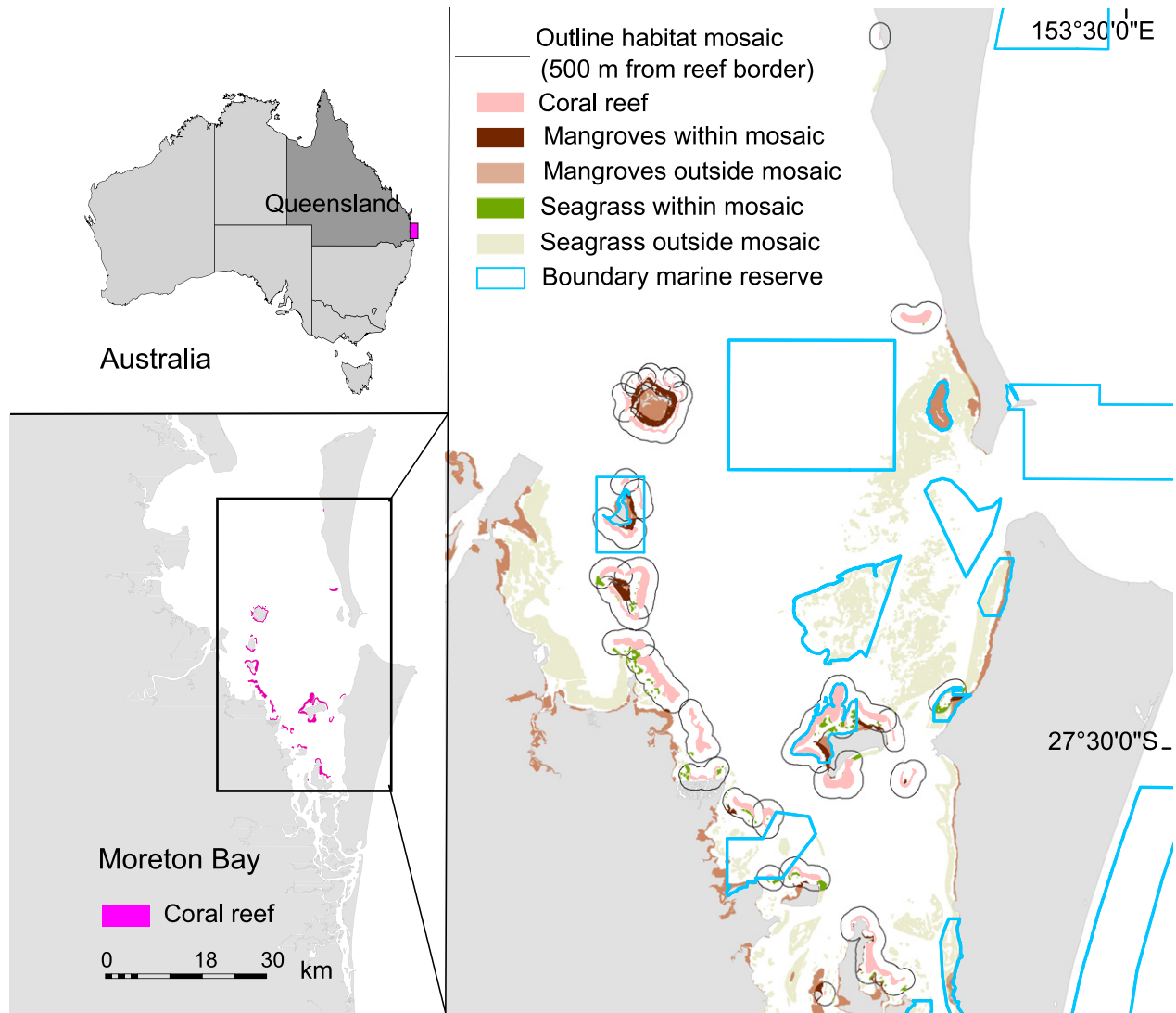


Fig. 1. Map of Australia with the location of Moreton Bay (left panel), and a detailed overview of Moreton Bay showing: marine reserves, habitats (coral reef, seagrass and mangroves), and the 29 habitat mosaics included in the model (right panel). Mosaics comprise a focal coral reef and nearby seagrass and/or mangroves within 500 m of the reef border (dark coloured). Seagrass and mangroves farther than 500 m from a coral reef are light coloured. [Colour figure can be viewed at wileyonlinelibrary.com].

2001; Queensland Government 2016). The third biophysical principle explicitly states that the placement of no-take areas should account for animal movements. As such, assessing the integration of connectivity in the reserve design may serve to improve the performance of the MPA against its own criteria and provide an approach that can be adapted to other protected areas, be they marine or terrestrial. Our model incorporated all habitat mosaics formed by coral reefs and proximate seagrass and mangroves; these occur mostly in the southern half of the bay (Fig. 1).

MODEL SPECIES

The two fish species we used as model organisms for analysis were orange-spotted grouper *Epinephelus coioides* (Hamilton, 1822) and yellowfin bream *Acanthopagrus australis* (Günther, 1859). These species were selected because they are (i) associated with coral reefs, mangroves and seagrass, (ii) represent a relevant range of scales at which reef-associated fish move, (iii) relatively

well studied with known home range distances and (iv) economically and socially important. Abundance of these fish species at reefs in our study area is not expected to depend heavily on larval dispersal and individuals are likely to belong to one population (Griffiths 2001; Harvey *et al.* 2012).

Orange-spotted groupers associate with structures of high complexity, including mangroves and coral reefs. The IUCN status of 'near threatened' makes their conservation a priority (IUCN 2015). Orange-spotted groupers are considered less mobile than bream, although their movement in Moreton Bay is less well studied. Tag-recapture studies indicate that juveniles and subadults exhibit high site fidelity over long periods: <9% of fish moving >10 m^{-d} with a maximum recorded movement of 2.2 km over 732 days (Sheaves 1993). This is within the previously reported range of '<5 km' for this genus (Green *et al.* 2015). Therefore, we selected a movement threshold of 1 km with a probability of 0.001 to further calculate the connection probabilities in the 1-km network (Sheaves 1993; Saura & Pascual-Hortal 2007).

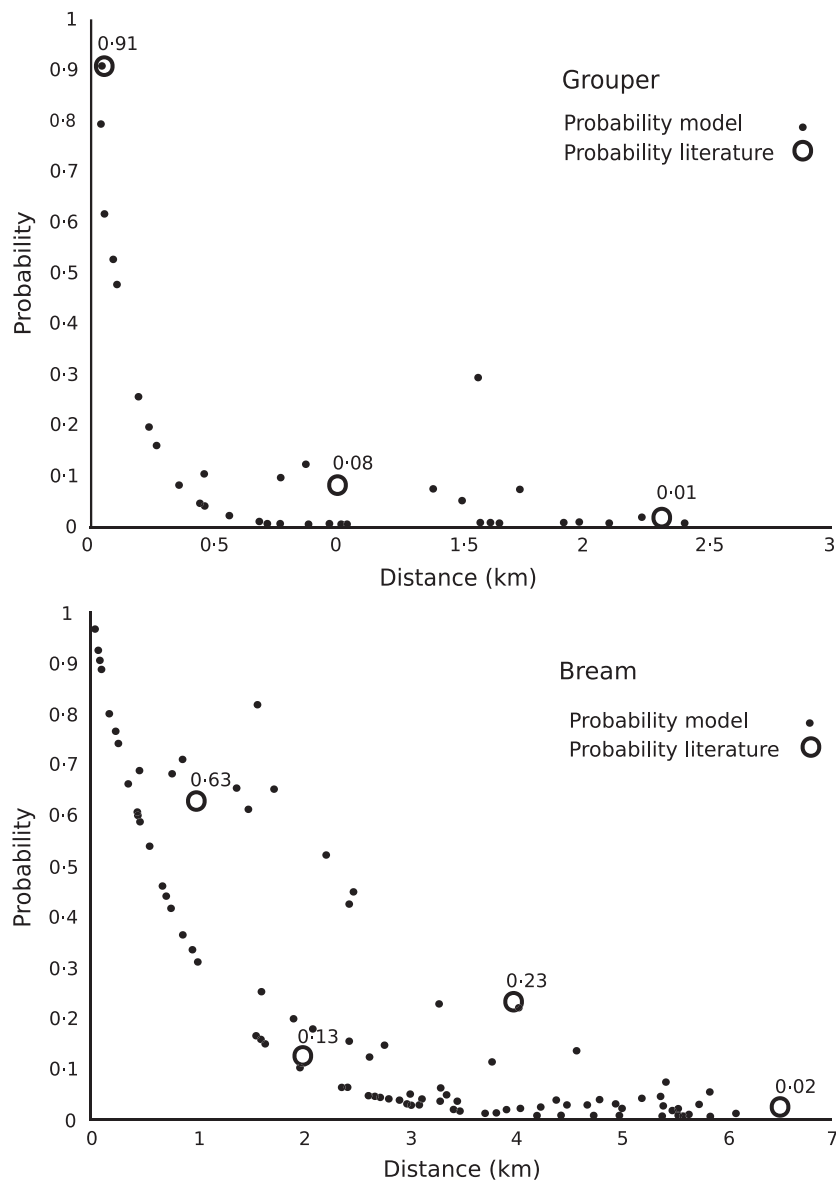


Fig. 2. Modelled movement probabilities and movement probabilities derived from the literature (Sheaves 1993; Butcher *et al.* 2010). The model matched probabilities according to specified threshold distances that represented the maximum home range movements and associated probability of the model species (Saura & Pascual-Hortal 2007). For grouper, the movement threshold was set to 1 km with a probability of 0.001 and for bream to 6 km and 0.001. Empirical values fall well within among the cloud of modelled range of probabilities.

Bream utilise a range of estuarine and near-shore habitats, but are commonly associated with coral reef, seagrass and mangrove habitats (Griffiths 2001; Olds *et al.* 2012a). Bream is a target species for recreational and commercial fishers (Broadhurst *et al.* 2005). Bream often show high mosaic fidelity over long periods, but tag-recapture studies show that they can also move long distances (>10 km) during spawning migrations (Pollock 1982; Sheaves 1993). A study using acoustic tags shows that regional-scale movements further than 1 km (up to 6 km in 12 h) can take place outside the spawning season (Butcher *et al.* 2010). For bream, the maximum threshold of movement was set to 6 km with a probability of 0.001 to further calculate the connection probabilities in the 6-km network (Saura & Pascual-Hortal 2007; Butcher *et al.* 2010).

NETWORK MODEL

Connectivity among habitat mosaics was analysed by developing a graph consisting of nodes and edges (Fig. 3) (Bunn, Urban & Keitt 2000). In defining nodes and edges, we made six

assumptions: (i) selected fish species use habitat mosaics (nodes) composed primarily of coral reef preferentially in the proximity of seagrass and/or mangroves (Olds *et al.* 2012a); (ii) seagrass and mangrove patches within 500 m distance from the reef border are considered connected for selected fish species (Olds *et al.* 2012a); (iii) selected fish species move among mosaics during routine movements of foraging and seeking refuge from predators (van Dyck & Bagueette 2005; Butcher *et al.* 2010; Green *et al.* 2015); (iv) distance is a proxy for travel costs (Turgeon *et al.* 2010); and (v) the probability of fish movement, and as a result connections (edges), decreases with increasing distance between patches and mosaics (Green *et al.* 2015).

NODES

The network included 29 nodes. Nodes consisted of mosaics, which comprised a group of habitat patches consisting of a focal coral reef and nearby seagrass and/or mangrove patches located within 500 m of reef borders (Fig. 3). Polygons indicated as reefs in the available GIS map were treated as separate reefs and were

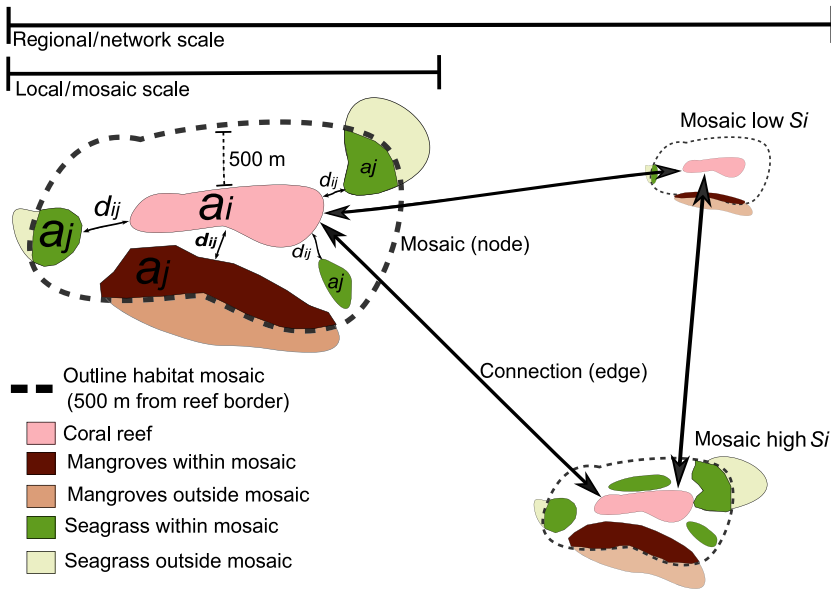


Fig. 3. Conceptual diagram of a habitat network formed by multiple habitat mosaics. The scale bars indicate conceptually the scales of connectivity modelled: local scale refers to connectivity within a single mosaic (node), while regional scale refers to connectivity among mosaics in the network based on connections (edges). [Colour figure can be viewed at wileyonlinelibrary.com].

the centre of nodes. Nodes are further referred to as mosaics because a mosaic generally refers to a group of habitat patches (Nagelkerken *et al.* 2015). Research in the study area showed that abundance of reef-associated fish is enhanced at reefs within 500 m to seagrass and/or mangroves (Olds *et al.* 2012a). Therefore, 500 m was chosen as the maximum distance from reef border to include seagrass or mangroves within mosaics (Olds *et al.* 2012a,b). Each mosaic was assigned an attribute value based on the distance-weighted habitat availability, which can be regarded as local, within-mosaic connectivity. To quantify this local connectivity, we calculated a separate proximity index, S_i , for seagrass and mangrove patches adjacent to coral reef. This index weighted the area of seagrass or mangroves (a_j) to their distance from the reef border (d_{ij}) (Fig. 3). The sum of the proximity values of individual patches of seagrass or mangrove within 500 m around the reef resulted in one proximity index (S_i) per habitat type ($S_i = \sum \frac{a_j}{d_{ij}^2}$). Area of a coral reef was included as a separate attribute value. The attributes were scaled to values between 0 and 1 to achieve relative values for the presence of habitat type in a mosaic. The three different attributes for seagrass, mangroves and coral reef were then summed to obtain a single attribute value for each mosaic that incorporated available habitat area and the within-mosaic connectivity (Fig. S1, Supporting Information). Prior to network analysis, these final attribute values of mosaics were scaled relative to each other to values ranging from 1 (for the largest value of S_i) to 0 (for the smallest value of S_i) (Fig. S1). The attribute values were subsequently used in the network analysis to calculate the regional connectivity. The calculation of the regional connectivity does not necessarily assume that one-third of each habitat is optimal, as a large reef lacking nearby seagrass or mangrove patches can have the same importance for connectivity as a small reef with nearby seagrass or mangrove patches. The species of interest in this study are coral reef-associated but can benefit from the proximity of nearby seagrass and mangroves. However, not all of these species depend on habitat variety and may instead be mostly affected by habitat structure, something that can be provided by a single type of habitat or a combination of habitats. Given our current level of knowledge about small-scale fish movements in this system, we preferred to incorporate local

connectivity with the proximity index and not make too many assumptions on movement behaviour. Benthic habitat maps for Moreton Bay (Queensland Government 2016) were used for area calculations in ArcGIS (ESRI 2015).

CONNECTIONS

Connections among mosaics were calculated from a negative exponential function of the interpatch reef border-to-reef border 'as-the-fish-swim' distances (Euclidean distances corrected for land barriers) (Saura & Pascual-Hortal 2007) (Figs 2 and S6).

Connections were measured from reef border to reef border because the coral reef is accessible during all tides, and movement among reef mosaics was assumed to start initially at the border of the reef. In total, the network comprised 406 connections between the 29 nodes (Fig. S2). We used the standard exponential decay model of the software Conefor 2.6 in which the sum of all possible routes between two nodes (maximum product probability) is used as the probability to calculate regional connectivity (Saura & Torné 2009; Fletcher *et al.* 2011).

NETWORK ANALYSIS

Our analysis of seascape connectivity focused on the landscape connectivity index PC , calculated with Conefor 2.6 (Saura & Torné 2009). Although there are other types of connectivity indices, such as node degree, this index is regarded as one of the most comprehensive and robust landscape connectivity indices for ranking individual habitat units and connections (Baranyi *et al.* 2011). The PC index integrates two scales of connectivity: within mosaics (local) and among mosaics (regional) based on the given mosaic attribute values and connections (Saura & Pascual-Hortal 2007). The connectivity value of an individual mosaic (dPC) is calculated as the change in PC when that mosaic is removed from the analysis. The dPC index is a proxy for habitat availability. However, its value is based on not only the attribute value of the mosaic (e.g. area, distance-weighted habitat area) but also the interaction between attribute values of mosaics and their position relative to other mosaics. The dPC index is the sum of

three complementary fractions that quantify these different aspects of connectivity: *dPCintra* (intramosaic connectivity), *dPCflux* (area-weighted dispersal flux based on position in the network and attributes of the focal mosaic) and *dPCconnector* (role as a stepping stone for movement through the network) (Table 1) (Saura & Rubio 2010). By including these three components, the *dPC* index provides a holistic characterisation of the connectivity of the system.

For both species, movement probabilities derived from literature fell within the range of modelled probabilities of connection. Modelled probabilities were mostly lower than the reference probabilities (Fig. 2), which indicate connectivity was not overestimated in our model. To incorporate the notion that species may move further during certain life-history stages, and to investigate whether our results are due to the choice of movement thresholds, we included a sensitivity analysis across a range of thresholds. We tested the sensitivity of *dPC* to the probabilistic model parameters by comparing the *dPC* rankings of mosaics and connections for movement thresholds that are 0.5, 1.5 and ≥ 2 times the two model thresholds using Pearson correlations coefficients. For grouper, we compared rankings of mosaics and connections based on 0.5, 1.5 and 3 km thresholds with the ranking of 1 km threshold to account for fish that remain within a mosaic and highly active fish. For bream, we compared rankings of mosaics and rankings of connections based on 3, 9 and 12 km thresholds with the ranking of a 6 km threshold. All correlations were strong (mosaics: minimum *R* value = 0.97, all *P* < 0.001; connections: minimum *R* value = 0.95, all *P* < 0.001), indicating that the results of our model are likely to be robust to divergence from selected thresholds (Table S1).

We tested for significant differences between rankings based on *dPC* values for thresholds of 1 and 6 km. The relationship between rankings was significantly positive both for mosaics (*R* value = 0.97, *P* < 0.001) and connections (*R* value = 0.84, *P* < 0.001) (Fig. S3A-B). For conservation managers, a single ranking would be an advantage over two conservation priority rankings. Therefore, given the similarity in rankings between thresholds, we averaged percentage *dPC* values from the two threshold distances. Rankings based on averaged *dPC* values were used to evaluate the reserve design with regard to habitat connectivity for fish. This was carried out by overlaying the map of Moreton Bay marine reserves with the ranked mosaics and connections. We then identified the number of protected mosaics

and connections and calculated the percentage of mosaic area within reserve boundaries, excluding areas of land, to evaluate the extent of protection of habitat connectivity. The representation of important connections in reserves was also tested by comparing the *dPC* values of connections within reserves to outside reserves with a Wilcoxon rank-sum test.

NETWORK MODEL ASSESSMENT

To assess the relationship of our network connectivity model and ecological patterns, we tested whether connectivity, as modelled by *dPC* and its fractions (*dPCintra*, *dPCflux* and *dPCconnector*), is positively associated with fish diversity, a conventional criterion in conservation planning. We hypothesised that diversity would have a stronger positive correlation with *dPC* and *dPCflux* as these two metrics account for multiple scales of connectivity compared to *dPCintra* or *dPCconnector*. Mosaics with high local and regional connectivity would offer habitat for species that exhibit strong mosaic fidelity as well as for species with high mobility, and thus harbour a high diversity of species, in contrast to *dPCintra* or *dPCconnector*, which describe connectivity based on either local or regional scale. We tested the relationship with empirical data on fish diversity (Shannon–Wiener index) in linear regression analyses (in R; R Development Core Team 2015). Fish diversity was calculated for nine of the 29 mosaics, based on abundance data of reef fish assemblages, published in Olds *et al.* (2012a). The index values were log (*x* + 1)-transformed to meet assumptions of normality.

Results

The 10 highest-ranked mosaics (of 29) in terms of *dPC* index values accounted for 86% of the sum of *dPC* values of all mosaics, which can be regarded as the regional seascape connectivity (Table 2, Figs S4 and S5). We chose to focus on the 10 highest-ranked mosaics to provide managers with a useful number of mosaics to prioritise, and readers with a clear description of our approach. Seven of these mosaics are located outside reserves (Table 2, Fig. 4). The three high-ranking mosaics situated within reserve boundaries are only partially represented (16–

Table 1. Definitions and equations of the graph theory-based index *Probability of Connectivity (PC)* and its three fractions derived from Saura & Rubio (2010)

$PC = \sum_{i=j}^n \sum_{i=j}^n a_i \times a_j \times P_{ij}^* = \frac{PC_{num}}{A_L}$	Index describing the habitat connectivity of an area
$dPC_k = 100 \times \frac{PC - PC_{remove,k}}{PC} = 100 \times \frac{\Delta PC_k}{PC}$ $dPC_k = dPCintra_k + dPCflux_k + dPCconnector_k$	Index describing the value for habitat connectivity of a landscape unit in an area
<i>dPCintra</i> $a_i \times a_j$ when $i = j = k(a_k^2)$	Based on the initial attribute values of a node (in this analysis <i>S_i</i> values of mosaics), and does not depend on the connectivity to other nodes
<i>dPCflux</i> $a_i \times a_j \times p_{ij}^*$ when $i = k$ or $j = k$ and $i \neq j$	Based on the number of incoming and/or outgoing connections and the initial attribute values of the node. This index can be regarded as a sink or source indicator
<i>dPCconnector</i> $a_i \times a_j \times p_{ij}^*$ when $i \neq k, j \neq k$	Based on the topology (position in the network) of a node and its irreplaceability as a link between other nodes. This index can be regarded as the stepping stone value of a node

Table 2. Ranking of mosaics based on their contribution to connectivity as quantified by the landscape connectivity index *dPC* (% of sum of all mosaics), and their level of representation. Percentages of representation are calculated as the area (m²) of a mosaic (excluding land) that is located within reserve boundaries. Lower-ranked mosaics partially within reserves are also included. See Fig. 4 for a visual display of mosaics

Mosaic rank	<i>dPC</i> (%)	Representation in reserves (%)
1	23	44
2	15	0
3	10	0
4	9	0
5	7	41
6	6	0
7	5	0
8	5	0
9	4	16
10	2	0
19	0.8	56
22	0.5	96
23	0.4	26
25	0.07	69
26	0.04	70

44%) by existing reserves and encompass 8% of the total area of mosaics in the network. Only 17% of the area of the 10 highest-ranked mosaics is currently represented inside reserves. Of the 19 remaining, lower-ranked mosaics, five are partially included, ranging between 26% and 96% spatial representation in reserves. In total, 16% of the entire area of mosaics of our model network is located inside reserves.

Of all 406 connections, the top 10 connections contributed to the bulk of regional connectivity (96%) as quantified by the *dPC* index (Table 3, Fig. S6). Only 1 of the 10 highest-ranking connections is located entirely within a reserve, and the remaining nine connections are currently outside reserve boundaries (Fig. 5). Using a threshold of 1 km, 38 connections (<9.4% of all connections) had a *dPC* > 0, indicating some contribution to connectivity and potential functional importance at this scale (Figs S2 and S6). For the 6 km threshold, 49 connections (<12.1% of all connections) had a *dPC* > 0 (Figs S2 and S6). Of all lower-ranked connections, five are entirely located within reserves, and three are partially represented (Table 3, Fig. 5). Connections inside marine reserve had significantly lower median *dPC* values than connections that were not included (Wilcoxon rank-sum test, $W = 348$, $P = 0.020$).

Fish species diversity shows the strongest relationship with *dPC* and *dPCflux* at movement thresholds above 6 km (Table 4). For *dPC*, the 1 km connectivity pattern shows a non-significant positive relationship with diversity index values ($R^2 = 0.38$, $P = 0.075$). This relationship becomes stronger and significant at higher movement thresholds (6 km: $R^2 = 0.51$, $P = 0.032$, 9 km: $R^2 = 0.57$, $P = 0.018$ and 12 km: $R^2 = 0.60$, $P = 0.014$). The

relationship between diversity index values and *dPCflux* values also increases with increasing movement threshold (Table 4). There is no relationship at a threshold of 1 km (Shannon–Wiener index: $R^2 = 0.01$, $P = 0.798$); however, at 6 km, fish species diversity is significantly positively associated with *dPCflux* values ($R^2 = 0.44$, $P = 0.050$), and the pattern based on the threshold of 12 km shows the strongest significant relationship of all connectivity patterns ($R^2 = 0.70$, $P = 0.005$). By contrast, connectivity patterns described by *dPCintra* are significantly positively related to diversity for all thresholds, but the association decreases in strength with increasing movement threshold (1 km: $R^2 = 0.54$, $P = 0.024$, 6 km: $R^2 = 0.50$, $P = 0.032$, 9 km: $R^2 = 0.49$, $P = 0.037$ and 12 km: $R^2 = 0.47$, $P = 0.042$) (Table 4). Connectivity patterns described by *dPCconnector* are negatively related to diversity for all thresholds, but this association is only significant for the 1 km connectivity pattern and decreases in strength with increasing movement threshold (1 km: $R^2 = 0.54$, $P = 0.024$, 6 km: $R^2 = 0.39$, $P = 0.073$, 9 km: $R^2 = 0.15$, $P = 0.303$ and 12 km: $R^2 = 0.03$, $P = 0.664$).

Discussion

Effective conservation planning needs to translate core and emerging concepts into tangible quantitative tools. Notwithstanding the fact that connectivity is theoretically recognised as an important feature in seascapes and that data on fish movement are generally available, marine reserve networks have rarely incorporated connectivity in their design (Magris *et al.* 2014; Green *et al.* 2015). This is largely due to a paucity of quantitative information on the multiple scales over which connectivity operates in seascapes, and the lack of appropriate metrics for its measurement and integration into conservation (Foley *et al.* 2010; Wedding *et al.* 2011; Olds *et al.* 2016). In this study, we demonstrate a method that provides such data for a coral reef seascape, the probability that mosaics are connected at a temporal scale that is used during routine movements (i.e. movements associated with daily activities) (van Dyck & Baguette 2005; Green *et al.* 2015). We show how using both local and regional connectivity for post-larval fish can result in numerical values for connectivity, which can be used to rank sites, and the connections among them.

In the reserve network considered here, the 10 mosaics that contribute most to connectivity are largely (83%) located outside existing reserve boundaries. This suggests that well-connected mosaics in Moreton Bay could be regarded as under-represented when considered against, for example, the recommendation that 20–40% of habitats should be represented in reserves (McLeod *et al.* 2009; Green *et al.* 2015). Another guiding principle in conservation planning is risk spreading, which advocates protection of at least three examples of a habitat within a reserve network (McLeod *et al.* 2009). Only three key mosaics fall partially (<50%) within reserves, and only

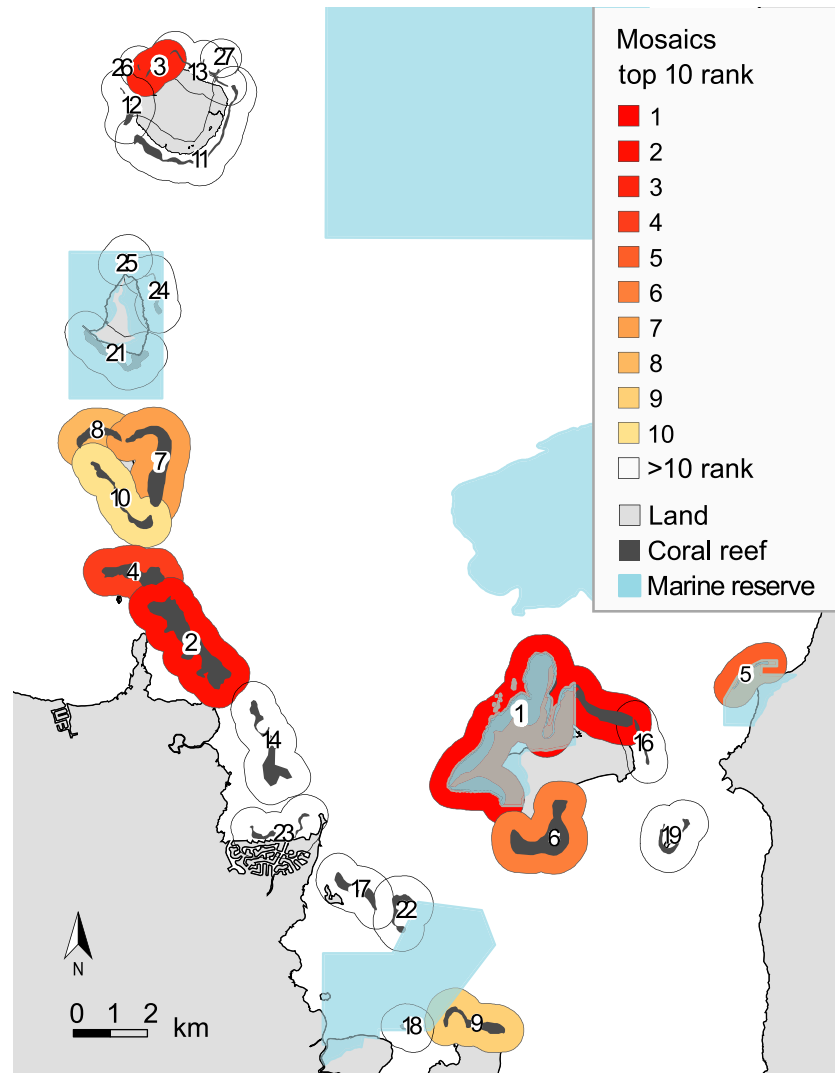


Fig. 4. Map showing the top 10 habitat mosaics in Moreton Bay. Mosaics are colour-coded according to their importance for connectivity as quantified by the landscape connectivity index dPC . The darkest colour (red) indicates the highest-ranked mosaic. The ranking is based on connectivity analyses (dPC values) averaged for two thresholds (1 and 6 km). The map also shows the locations of marine reserves. [Colour figure can be viewed at wileyonlinelibrary.com].

one key regional connection between mosaics is inside a reserve. Our results suggest that connectivity for reef-associated fish in Moreton Bay is currently insufficiently represented spatially and, therefore, protected both in terms of representation and risk spreading.

Finding efficient ways to protect multiple species, rather than needing management plans for individual species, is a major challenge in spatial conservation planning (Rayfield *et al.* 2016). One solution is to plan for so-called surrogate species, which share habitats and home ranges with many other species (Olds *et al.* 2014). Alternatively, the average spatial requirements of multiple species can be used to evaluate protection of connectivity, as has been carried out for terrestrial mammals (Minor & Lookingbill 2010). Here, we aimed to build a model based on the habitat needs and movement biology of two important native fish species of which the movement scale is representative of a wide range of other species, while distinguishing scale-dependent connectivity patterns (Green *et al.* 2015). Consequently, our approach shows similarities to both management solutions. Our model is therefore likely to represent the movement

biology of a substantial proportion of fish species and may have wide application in reef seascapes.

The movement of animals is important for population dynamics and ecosystem-wide processes; consequently, connectivity patterns are also often related to ecosystem measures such as diversity (Pittman & McAlpine 2003; Kool, Moilanen & Treml 2013). However, in many studies, connectivity is either quantified at the patch or mosaic (local) scale or the landscape (regional) scale (Wedding *et al.* 2011; Magris *et al.* 2014). In this study, we incorporated two spatial scales in a habitat connectivity analysis through the proximity index S_i and the landscape connectivity index dPC , which accounted for the interaction between habitat area and the position of a mosaic relative to the other mosaics. In addition, we examined separate aspects of connectivity through different fractions of dPC . Previous studies that used connectivity indices closely related to dPC reported a positive relationship between connectivity and species richness for intermediate and higher movement thresholds in freshwater environments (Ribeiro *et al.* 2011; Ishiyama, Akasaka & Nakamura

Table 3. Ranking of the top 10 ranked connections among mosaics based on their contribution to connectivity as quantified by the index *dPC* (% of sum of all connections), and the level of representation (full, partially or none). Also listed are connections that ranked lower or have no *dPC* value and could not be ranked (indicated with –), but are represented within reserves. See Fig. 5 for visual display of connections

Connection	Rank	<i>dPC</i> (%)	Representation in reserves (%)
2–4	1	19	None
8–7	2	17	None
3–13	3	13	None
6–1	4	11	None
11–13	5	11	None
16–1	6	9	None
10–7	7	5	None
14–2	8	5	None
4–10	9	4	None
18–9	10	2	Full
21–8	34	<0.01	Partial
18–22	29	<0.01	Full
25–24	27	<0.01	Full
21–24	19	<0.01	Full
9–22	17	<0.01	Full
25–21	–	<0.01	Full
18–17	–	<0.01	Partial
9–17	–	<0.01	Partial

2014). Our study is novel in finding this relationship for post-larval fish in a marine system.

It is common for managers to have data on surrogate or umbrella species that may be used to represent related species in conservation planning (Olds *et al.* 2014). However, it can be a considerable challenge to use these data in a manner that ensures other species are indeed protected as well. As such, it is important to identify if available surrogate information does correlate with underlying processes that it is being used to represent. When comparing the patterns of fish diversity and connectivity of mosaics, we found that the connectivity indices *dPC* and *dPCflux* are positively related to fish diversity for the 6, 9 and 12 km thresholds, yet there was no relationship for the 1 km threshold. Conversely, the index *dPCintra* calculated for 1 km resulted in a connectivity pattern that is significantly positively related to fish diversity and the index *dPCconnector* showed a significantly negative relationship. Our results suggest that managers wishing to use connectivity patterns as a predictor of diversity should examine different connectivity metrics depending on the movement scale of a focal species or the data available, for example those showing site fidelity or having high mobility. This is consistent with theoretical predictions of the importance of multiple indices (Saura & Rubio 2010). In our study, this implies that at intermediate (6–12 km) or large-scale movement distances (>12 km), the indices *dPC* and *dPCflux* best describe areas that are also valuable for other reef-associated fish in Moreton Bay.

The *dPC* index and its fractions were specifically developed to analyse and prioritise landscape connectivity (i.e.

habitat availability), to supply information on multiple scales of connectivity and to value both areas and connections (Saura *et al.* 2014). While selecting one of the fractions of *dPC* for the analysis would enable prioritisation of a specific aspect of connectivity, we chose *dPC* to evaluate the importance of mosaics in the broadest sense of connectivity measures. In the situation that managers need to plan for connectivity in a comprehensive way but with little data available, the *dPC* index remains in our opinion the most suitable metric for prioritisation. It could be developed further by incorporating potential interactive effects of different habitat components, which may account for synergistic effects of different combinations of habitat types in the mosaics.

More complex, dynamic models can be useful in marine conservation planning (Kininmonth *et al.* 2011) and have been shown to perform better in estimating costs and benefits of marine reserves for fishing in the long term. Nonetheless, static models can perform well for shorter term planning, especially for non-directional connectivity and in areas that are well managed (Brown *et al.* 2015); both are applicable in Moreton Bay. In this study, a static model was considered appropriate because our objective was to identify areas that are likely to be of high importance for fish movement and thus of priority for conservation, which is a different aim to modelling the dynamics of fish distributions over time. Although the *dPC* index is static, it still accounts for some changes in connectivity by quantifying explicitly the stepping stone role (irreplaceability) of mosaics.

From our analysis, it is evident that important connections are associated with important mosaics. Prioritising areas that are likely to facilitate fish movement across local seascapes and connect mosaics that are important for regional connectivity would, therefore, have the most impact on how well connectivity is represented in the system. Greatest improvements to representing regional connectivity in conservation will occur where connections among mosaics ranked in the top 10 (i.e. orange arrows number 1, 2, 4, 7, 9) are incorporated into future marine reserves (Fig. 5). At present, some marine reserves include mosaics that are not particularly important for local- or regional-scale connectivity. Relocating these reserves to other reef seascapes would improve the representation of connectivity, and potentially reserve performance, without having to increase the total area of reserves or decrease the level of representation afforded to other seascapes.

Connectivity is, however, not the only principle for conservation planning, and we view the ranking of mosaics and connections for conservation as complementary to other criteria (socio-economic and biophysical) (Watts *et al.* 2009; Pouzols & Moilanen 2014). Results from this study could for example be used in reserve-planning programs such as Marxan, which uses values of planning units in its calculations. With the method used in our study, values can be assigned to planning units for their role in regional connectivity. The management of the Moreton Bay Marine

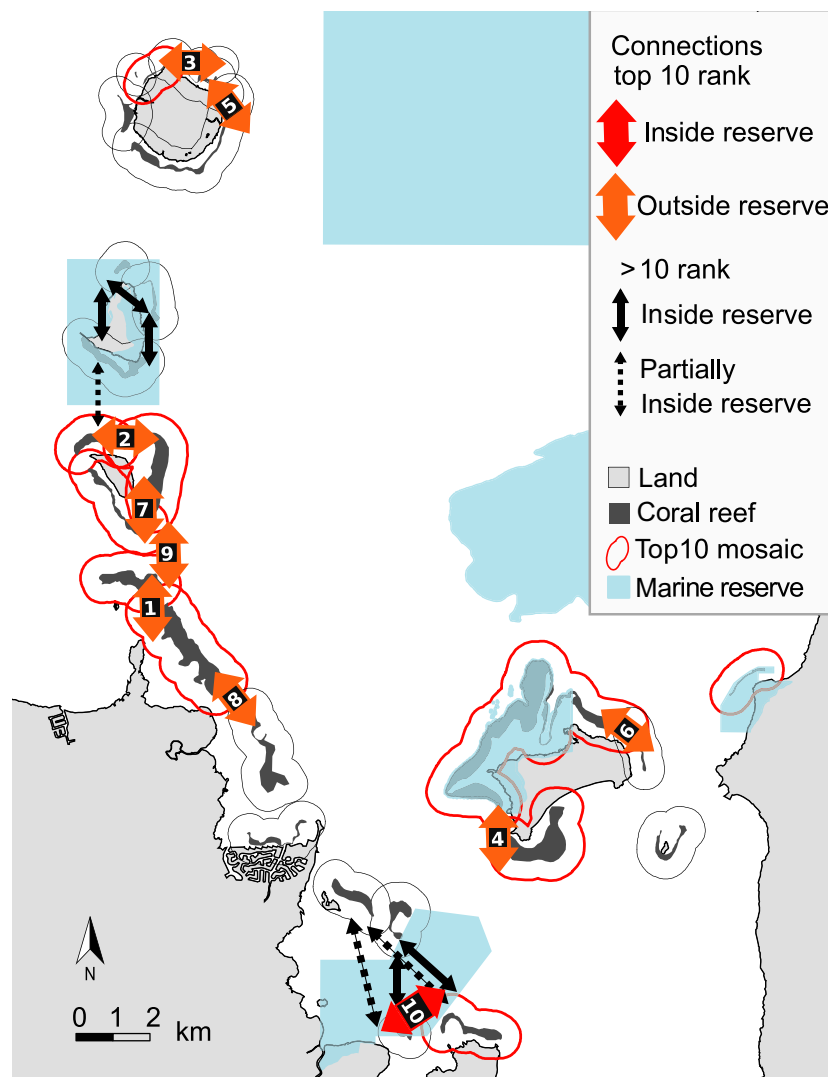


Fig. 5. Map showing the top 10 regional connections among mosaics that contribute most to connectivity, as quantified by the landscape connectivity index dPC , but fall outside reserves (orange) and the one connection that is located inside a reserve (red). Connections that contribute less to connectivity, but are inside (black) or partially inside (dashed black) reserves are also displayed. [Colour figure can be viewed at wileyonlinelibrary.com].

Table 4. Results of linear regressions between the connectivity index dPC , its three fractions (dPC_{intra} , dPC_{flux} and $dPC_{connector}$) based on movement thresholds 0.5–12 km, and fish diversity as calculated with the Shannon–Wiener index. Significant relationships with a $R^2 > 0.50$ are in bold. Connectivity patterns described by indices dPC , dPC_{intra} , dPC_{flux} have a positive relationship with the pattern of fish diversity except for the pattern described by $dPC_{connector}$, which has a negative relationship

Movement threshold (km)	dPC		dPC_{intra}		dPC_{flux}		$dPC_{connector}$	
	R^2	P	R^2	P	R^2	P	R^2	P
0.5	0.48	0.038	0.54	0.023	0.01	0.767	0.54	0.024
1	0.38	0.075	0.54	0.024	0.01	0.798	0.54	0.024
1.5	0.36	0.089	0.54	0.025	0.05	0.562	0.54	0.024
3	0.40	0.068	0.52	0.028	0.20	0.232	0.51	0.030
6	0.51	0.032	0.50	0.032	0.44	0.050	0.39	0.073
9	0.57	0.018	0.49	0.037	0.62	0.012	0.15	0.303
12	0.60	0.014	0.47	0.042	0.70	0.005	0.03	0.664

Park aims to be adaptive and take into account scientific evidence when the zoning plan is reviewed. The current design dates from 2008, and this study provides additional evidence to be taken up in future reviews.

In conclusion, we incorporated local- and regional-scale connectivity in a model and then used it to evaluate how

well existing marine reserves incorporate key seascape connections. While connectivity is a guiding principle for the design of marine reserve networks world-wide, decision-makers often lack quantitative information about how to prioritise areas on this basis (Foley *et al.* 2010; Magris *et al.* 2014). Here, we show that key local and

regional seascape connections are under-represented in the reserve network in Moreton Bay, and discuss potential opportunities for improving reserve design. We focused on coral reef seascapes, but our approach is applicable to other heterogeneous landscapes and can improve how connectivity is integrated into conservation elsewhere in the sea, and on land.

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Data accessibility

Data on model input values are included in the supporting information (Fig. S1).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Pearson correlation between two rankings of mosaics, and Pearson correlation between two rankings of connections.

Fig. S1. Attribute values for each habitat mosaic based on intramosaic habitat connectivity.

Fig. S2. Graphs showing networks with all, 6 and 1 km connections.

Fig. S3. A-B. Pearson correlation between rankings of mosaics and connections based on two movement thresholds.

Fig. S4. The *dPC* values of each mosaic for two movement thresholds.

Fig. S5. The *dPC* values separated in fractions.

Fig. S6. The *dPC* value of each connection for two movement thresholds.