Prioritizing 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 are 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 to 6 km), connectivity (quantified by the index Probability of Connectivity (dPC)) explained 51–60 % of species diversity. At smaller home ranges (0 to 1 km) species diversity was associated closely with intra-mosaic connectivity quantified by the index dPCintra.

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 ten 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:** fish movement, connectivity, marine conservation, marine reserves, network model, seascape, conservation planning, coral reef

**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 sub-populations between distinct habitats (McClanahan et al. 2012; Saura et al. 2014). The importance of quantifying multi-scale and multipurpose connectivity has become 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; Liquete 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 is 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 (Treml et al. 2008; Beger et al. 2010). Multi-species larval dispersal has also been modelled in combination with social connectivity using network analysis (Treml 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 multi-scale 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 multi-species 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 2001; Queensland Government 2015). 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: 1) associated with coral reefs, mangroves and seagrass, 2) represent a relevant range of scales at which reef-associated fish move, 3) relatively well-studied with known home-range distances, and 2) 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 sub-adults exhibit high site fidelity over long periods: < 9% of fish moving > 10 m d

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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).

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 by 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 hours) 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: 1) 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); 2) seagrass and mangrove patches within 500 m distance from the reef border are considered connected for selected fish species (Olds et al. 2012a); 3) selected fish species move among mosaics during routine movements of foraging and seeking refuge from predators (Van Dyck & Baguette 2005; Butcher et al. 2010; Green et al. 2015); 4) distance is a proxy for travel costs (Turgeon et al. 2010); and 5) 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 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 beds 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 (Supporting information Fig. S1). 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 $S_i$) (Supporting information 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 (source: Queensland Government) were used for area calculations in ArcGIS (ESRI 2015).

**Connections**

Connections among mosaics were calculated from a negative exponential function of the inter-patch reef edge-to-reef edge ‘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 are 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 (Supporting information 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 with (Saura & Torné 2009; Fletcher et al. 2011).

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Network analysis

Our analysis of seascape connectivity focused on the landscape connectivity index ‘Probability of Connectivity’ (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 not only based on the attribute value of the mosaic (e.g. area, distance weighted habitat area) but 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 (intra-mosaic 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 if 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 $\geq$ 2 times the two model thresholds using Pearson correlations coefficients. For grouper, we compared rankings of mosaics and connections based on 0.5 km, 1.5 km 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 km, 9 km 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 (Supporting information Table S1).

We tested for significant differences between rankings based on $dPC$ values for thresholds of 1 km 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, $P < 0.001$) (Supporting information 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 regards to habitat connectivity for fish. This was done 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.

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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 ($dPC_{intra}$, $dPC_{flux}$ and $dPC_{connector}$), 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 $dPC_{flux}$ as these two metrics account for multiple scales of connectivity compared to $dPC_{intra}$ or $dPC_{connector}$. 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 $dPC_{intra}$ or $dPC_{connector}$, 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 9 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 ten highest-ranked mosaics (out 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, Supporting information Figs S4 & S5A-B). We chose to focus on the ten 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 (16-44%) by existing reserves, and encompass 8% of the total area of mosaics in the network. Only 17% of the area of the ten
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 ten connections contributed to the bulk of regional connectivity (96%) as quantified by the $dPC$ index (Table 3, Supporting information Fig. S6). Only one of the ten 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 (Supporting information Figs S2 & S6). For the 6 km threshold, 49 connections (< 12·1% of all connections) had a $dPC > 0$ (Supporting information Figs S2 & 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 $dPC_{flux}$ 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 $dPC_{flux}$ 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 $dPC_{flux}$ 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 $dPC_{intra}$ 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 $dPC_{connector}$ 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 recognized 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 ten 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 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 done 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
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 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 this 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 km, 9 km and 12 km thresholds, yet there was no relationship for the 1 km threshold. Conversely, the index

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$dPCintra$ 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 and 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 ten (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

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values can be assigned to planning units for their role in regional connectivity. The management of the Moreton Bay Marine 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 worldwide, 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).
Supporting information

Additional Supporting Information can be found with 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 intra-mosaic habitat connectivity.

Fig. S2. Graphs showing networks with all, 6 km 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. S5A-B. The dPC values separated in fractions.

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

References


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

\[ PC = \sum_{i=j}^{n} \sum_{i=j}^{n} a_i \times a_j \times p_{ij}^* = \frac{PC_{num}}{A_k^2} \]

Index describing the habitat connectivity of an area.

\[ dPC_k = 100 \times \frac{PC_{intra}}{PC} = 100 \times \Delta PC_k \]

Index describing the value for habitat connectivity of a landscape unit in an area.

**dPCintra**

\[ a_i \times a_j \]

when \( i = j = k \) (\( a_k^2 \))

Based on the initial attribute values of a node (in this analysis \( S_i \) values of mosaics), and does not depend on the connectivity to other nodes.

**dPCflux**

\[ a_i \times a_j \times p_{ij} \]

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.

**dPCconnector**

\[ a_i \times a_j \times p_{ij} \]

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 steppingstone 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 ($m^2$) 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.

<table>
<thead>
<tr>
<th>Mosaic rank</th>
<th>dPC (%)</th>
<th>Representation in reserves (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>23</td>
<td>44</td>
</tr>
<tr>
<td>2</td>
<td>15</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>9</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>7</td>
<td>41</td>
</tr>
<tr>
<td>6</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>7</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>8</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>9</td>
<td>4</td>
<td>16</td>
</tr>
<tr>
<td>10</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>19</td>
<td>0.8</td>
<td>56</td>
</tr>
<tr>
<td>22</td>
<td>0.5</td>
<td>96</td>
</tr>
<tr>
<td>23</td>
<td>0.4</td>
<td>26</td>
</tr>
<tr>
<td>25</td>
<td>0.07</td>
<td>69</td>
</tr>
<tr>
<td>26</td>
<td>0.04</td>
<td>70</td>
</tr>
</tbody>
</table>
**Table 3.** Ranking of the top ten 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.

<table>
<thead>
<tr>
<th>Connection</th>
<th>Rank</th>
<th>$dPC$ (%)</th>
<th>Representation in reserves (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>4 to 10</td>
<td>9</td>
<td>&lt; 0·01</td>
<td>partial</td>
</tr>
<tr>
<td>18 to 22</td>
<td>29</td>
<td>&lt; 0·01</td>
<td>full</td>
</tr>
<tr>
<td>25 to 24</td>
<td>27</td>
<td>&lt; 0·01</td>
<td>full</td>
</tr>
<tr>
<td>21 to 24</td>
<td>19</td>
<td>&lt; 0·01</td>
<td>full</td>
</tr>
<tr>
<td>9 to 22</td>
<td>17</td>
<td>&lt; 0·01</td>
<td>full</td>
</tr>
<tr>
<td>25 to 21</td>
<td>-</td>
<td>&lt; 0·01</td>
<td>full</td>
</tr>
<tr>
<td>18 to 17</td>
<td>-</td>
<td>&lt; 0·01</td>
<td>partial</td>
</tr>
<tr>
<td>9 to 17</td>
<td>-</td>
<td>&lt; 0·01</td>
<td>partial</td>
</tr>
</tbody>
</table>
Table 4. Results of linear regressions between the connectivity index $dPC$, its three fractions ($dPC_{intra}$, $dPC_{flux}$, $dPC_{connector}$) 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.

<table>
<thead>
<tr>
<th>Movement threshold (km)</th>
<th>$dPC$</th>
<th>$dPC_{intra}$</th>
<th>$dPC_{flux}$</th>
<th>$dPC_{connector}$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$R^2$</td>
<td>$P$</td>
<td>$R^2$</td>
<td>$P$</td>
</tr>
<tr>
<td>0.5</td>
<td>0.48</td>
<td>0.038</td>
<td>0.54</td>
<td>0.023</td>
</tr>
<tr>
<td>1</td>
<td>0.38</td>
<td>0.075</td>
<td>0.54</td>
<td>0.024</td>
</tr>
<tr>
<td>1.5</td>
<td>0.36</td>
<td>0.089</td>
<td>0.54</td>
<td>0.025</td>
</tr>
<tr>
<td>3</td>
<td>0.40</td>
<td>0.068</td>
<td>0.52</td>
<td>0.028</td>
</tr>
<tr>
<td>6</td>
<td>0.51</td>
<td>0.032</td>
<td>0.50</td>
<td>0.032</td>
</tr>
<tr>
<td>9</td>
<td>0.57</td>
<td>0.018</td>
<td>0.49</td>
<td>0.037</td>
</tr>
<tr>
<td>12</td>
<td>0.60</td>
<td>0.014</td>
<td>0.47</td>
<td>0.042</td>
</tr>
</tbody>
</table>
Figures

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 (darker coloured). Seagrass and mangroves farther than 500 m from a coral reef is lighter coloured.
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.
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), whilst regional scale refers to connectivity among mosaics in the network based on connections (edges).
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 km and 6 km). The map also shows the locations of marine reserves.
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.