



Predicting reef fish connectivity from biogeographic patterns and larval dispersal modelling to inform the development of marine reserve networks



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ABSTRACT

Developing networks of no-take marine reserves is often hindered by uncertainty in the extent to which local marine populations are connected to one another through larval dispersal and recruitment (connectivity). While patterns of connectivity can be predicted by larval dispersal models and validated by empirical methods, biogeographic approaches have rarely been used to investigate connectivity at spatial scales relevant to reserve networks (10's–100's of km). Here, species assemblage patterns in coral reef fish were used together with an individual-based model of dispersal of reef fish larvae to infer patterns of connectivity in a ~300 km wide region in the Philippines that included the Bohol Sea and adjacent bodies of water. A dominant current flows through the study region, which may facilitate connectivity among >100 no-take reserves. Connectivity was first investigated by analysing data on the presence/absence of 216 species of reef fish and habitat variables across 61 sites. Hierarchical clustering of sites reflecting species assemblage patterns distinguished a major group of sites in the Bohol Sea (Bray–Curtis similarity >70%) from sites situated in adjacent bodies of water (bays, channels between islands and a local sea). The grouping of sites could be partly explained by a combination of degree of embayment, % cover of sand and % cover of rubble (Spearman rank correlation, $\rho_w = 0.42$). The individual-based model simulated dispersal of reef fish larvae monthly for three consecutive years in the region. The results of simulations, using a range of pelagic larval durations (15–45 days), were consistent with the species assemblage patterns. Sites in the model that showed strongest potential connectivity corresponded to the majority of sites that comprised the Bohol Sea group suggested by hierarchical clustering. Most sites in the model that exhibited weak connectivity were groups of sites which had fish assemblages that were least similar to those in the Bohol Sea group. Concurrent findings from the two approaches suggest a strong influence of local oceanography and geography on broad spatial patterns of connectivity. The predictions can be used as an initial basis to organise existing reserves to form ecologically meaningful networks. This study showed that species assemblage patterns could be a viable supplementary indicator of connectivity if used together with predictions from a larval dispersal model and if the potential effect of habitat on the structuring of species assemblages is taken into consideration.

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1. Introduction

Connectivity is often defined as the linking of local marine populations through the dispersal of individuals during their pelagic larval phase and their subsequent incorporation to the recipient population (recruitment) as juveniles or adults

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Table 1

Framework to infer connectivity between two sites using data on larval dispersal predicted by a biophysical model and data on habitat and species assemblage structure measured by field surveys. The final column lists possible conclusions about connectivity between the two sites.

Case	Larval exchange predicted by biophysical model	Measured habitat characteristics	Measured species assemblage structure	Possible conclusions
1	Strong	Similar	Similar	Connectivity likely to be strong
2	Strong	Different	Dissimilar	Connectivity is questionable (may be weak for many species due to lack of recruitment habitat)
3	Weak	Similar	Dissimilar	Connectivity likely to be absent or weak (species assemblages at each site differ because of low levels of larval exchange)
4	Weak	Different	Dissimilar	Connectivity likely to be absent or weak (species assemblages at each site differ because of low levels of larval exchange and different habitats)
5	Strong	Similar	Dissimilar	- Failure to account for the most influential post-recruitment process (e.g., fishing mortality)
6	Strong	Different	Similar	- Failure to account for the most influential habitat parameter/s
7	Weak	Similar	Similar	- Failure of biophysical model to predict connectivity accurately
8	Weak	Different	Similar	- Failure to measure species assemblage accurately

(Sale et al., 2005). The spatial extent of such connections is a central issue in understanding population genetic structuring and broad-scale distribution patterns of marine species with a dispersive larval phase (Planes, 2002; Rocha et al., 2002; Kool et al., 2011). The strength of connectivity within ecological time scales may strongly determine whether local populations will persist or decline amidst natural and man-made disturbances (Cowen et al., 2006; Burgess et al., 2014). Thus, patterns of connectivity have important implications for designing and evaluating the performance of spatially-explicit marine management interventions, particularly the use of networks of no-take marine reserves (Gaines et al., 2010; Green et al., 2014; Grorud-Colvert et al., 2014).

The interest to design marine reserve networks that consider connectivity has grown rapidly in recent years (Almany et al., 2009; McCook et al., 2009; Gaines et al., 2010; Treml and Halpin, 2012; Green et al., 2014). However, empirical data on ecologically meaningful patterns of larval dispersal are not easy to obtain at the likely operational spatial scales of marine reserve networks (10's–100's of km). Connectivity is inherently difficult to measure in the field due to the small size, difficulty of sampling, complex biology and behaviour of larvae interacting with the dynamic nature of the oceanic environment (e.g., Leis, 2006; Paris et al., 2007). Inferences about connectivity may be gained by applying a suite of approaches ranging from genetic methods (e.g., Pinsky et al., 2010; Harrison et al., 2012), isotope analysis (e.g., Chittaro and Hogan, 2013) and biophysical modelling of larval dispersal (e.g., James et al., 2002; Cowen et al., 2006; Paris et al., 2007; Treml and Halpin, 2012). Considerations about connectivity may be best integrated into the design of reserve networks by using predictions generated by larval dispersal models and cross-validated by empirical studies (Cudney-Bueno et al., 2009; Jones et al., 2009).

Biogeographic studies may help to elucidate patterns of connectivity at a range of spatial scales (10's–1000's of km) similar to those predicted by biophysical models (Jones et al., 2009). However, some biogeographic approaches (e.g., phylogeography) may be more appropriate to infer the presence or absence of connectivity over long time scales (100's–1000's of years) that are less relevant to ecology (Planes, 2002; Rocha et al., 2002). A straightforward and potentially useful biogeographic approach is to infer spatial patterns of connectivity from the structuring of species assemblages at regional scales. Although it is usually not possible to determine precisely the time scale of connectivity from species assemblage patterns, this approach has been used to argue for the presence or absence of connectivity in coral reef fish at spatial scales of 100's of km on the Great Barrier Reef and in the Red Sea (Williams et al., 1986; Roberts, 1991). However, a dearth of studies prevents an appraisal of the effectiveness of species assemblage

patterns as an indicator of connectivity at spatial scales that are most applicable to marine reserve networks.

The usefulness of species assemblage patterns as an indicator of connectivity is dependent upon the degree to which demographic patterns determined by larval supply are modified by ecological processes occurring after recruitment. In coral reef fish, demographic patterns may be strongly influenced by habitat selection and mortality during the pelagic larval, benthic juvenile and adult stages (Jones, 1991; Pratchett et al., 2008). Abundance and species diversity of adults are often strongly correlated with habitat availability and structure (e.g., Carpenter et al., 1981; Friedlander et al., 2003; Emslie et al., 2010). Thus, if species assemblage patterns are to be used to infer connectivity, the potential influence of both larval supply and habitat must be considered.

For two hypothetical sites in question, the presence or absence of significant larval exchange between these sites and the characteristics of the habitat at each site may result in either similar or dissimilar species assemblages. Using the framework outlined in Table 1, connectivity between two sites may be better inferred on the basis of information on the strength of larval exchange between the sites predicted by a biophysical model and the characteristics of species assemblages and habitats between the sites measured by field surveys. Connectivity is likely to be significant if species assemblages and habitats are similar between sites and the model predicts strong larval exchange (Table 1, Case 1). However, conclusions about connectivity become questionable if the species assemblages and habitats are dissimilar between sites but the model predicts high levels of larval exchange between the sites (Table 1, Case 2). Connectivity is likely to be absent or not significant when larval exchange is predicted by the model to be weak and species assemblages are dissimilar between sites, whether habitats at the two sites are similar or are different (Table 1, Cases 3 and 4). The four preceding cases assume that the measurement of habitat parameters, representation of species assemblage patterns and predictions made by the larval dispersal model are all reasonably accurate. All four preceding cases also assume that habitat is the most influential post-recruitment factor structuring species assemblages. Failure of any one of these assumptions may be suspected in four other cases (Table 1, Cases 5–8). Note that in this framework, conclusions about connectivity would be problematic if fishing pressure is extremely high for a wide range of targeted species and these species are included in the analysis. This is because high fishing mortality may considerably alter species assemblage structure (Pauly et al., 1998). Thus, the available information could often reflect Case 5 (Table 1).

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