



RESEARCH
PAPER

Mangrove-reef connectivity promotes the effectiveness of marine reserves across the western Pacific

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ABSTRACT

Aim To evaluate the potential of habitat connectivity to promote the effectiveness of marine reserves. We used heterogeneous reef seascapes as a model system to examine the potential interaction of reserves and mangrove-reef connectivity and compared the magnitude of these effects across the western Pacific Ocean.

Location The tropical and subtropical western Pacific, including the Solomon Islands, Great Barrier Reef and Moreton Bay, Australia.

Methods We quantified fish densities on coral reefs (38 sites) and in mangrove forests (19 sites) across seven marine reserves and twelve unprotected control locations. Fish assemblages were in seascapes supporting either adjacent reefs and mangroves or isolated reefs. For each reserve-control comparison, we evaluated the potential interactive effects of habitat connectivity on species richness and densities of harvested species, functional groups, families and individual species. We then examined the influence of spatial variation in reserve attributes, seascape heterogeneity and latitude on the magnitude of reserve-connectivity effects.

Results Snappers (Lutjanidae) and rabbitfish (Siganidae) were more abundant on reserve reefs close to mangroves in all regions. These interactive effects also enhanced the abundance of sweetlip (Haemulidae), bream (Sparidae), harvested fish, herbivores and piscivores and species richness in two of the three regions examined. Spatial variation in the magnitude of reserve-connectivity effects was explained by differences among reserves in seascape variables (i.e. area of mangroves and reef, duration of mangrove inundation and distance to rivers) but not by reserve attributes (i.e. age, size, poaching) or latitude.

Main conclusions Habitat connectivity improved the effectiveness of reserves across the western Pacific Ocean. We recommend that heterogeneous landscapes with high-habitat connectivity should be viewed as high priorities for conservation. By improving our understanding of connectivity, and through its explicit incorporation into conservation, we may have greater success in restoring biodiversity and functioning of ecosystems.

Keywords

Australia, coral reef, Coral Triangle, fish, Great Barrier Reef, landscape ecology, mangroves, marine reserve, Solomon Islands.

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INTRODUCTION

We establish and manage reserves to restore biodiversity and maintain resilient, functioning ecosystems (Estes *et al.*, 2011). Our success or failure will depend, in part, on our ability to

incorporate difficult concepts, like connectivity, into strategies for ecosystem-based management (e.g. Massol *et al.*, 2011) and spatial conservation planning (e.g. Foley *et al.*, 2010). Connectivity is a fundamental component of many ecological paradigms (Sheaves, 2009), it is central to the distribution of all

species, and is critical for maintaining ecosystem functions (Lindenmayer *et al.*, 2008). By linking ecological processes and food webs across landscapes (Polis *et al.*, 1997; Nyström & Folke, 2001), it may also confer ecosystems with resilience (*sensu* Cumming, 2011), which is the capacity to absorb recurrent perturbations and regenerate without slowly degrading or changing state (Hughes *et al.*, 2010). Consequently, understanding and enhancing connectivity is necessary for conservation (Hodgson *et al.*, 2009). It provides the mechanism for reserves to sustain exploited fish populations beyond their borders (McCook *et al.*, 2009), and is paramount to reversing human-mediated trophic cascades and their effects on ecosystem resilience (Estes *et al.*, 2011). For this reason, connectivity is now integrated into strategies for conservation planning and environmental management, and recently, has been shown to improve the potential of reserves to enhance populations of exploited consumers (Olds *et al.*, 2012a) and subsidize the supply of larvae to fished populations (Harrison *et al.*, 2012).

Connectivity is governed by the dispersal capabilities of individual species and is a function of the area, quality and spatial arrangement of habitats (Hodgson *et al.*, 2009). The term is frequently used to describe biological and physical linkages among habitats, landscapes and ecosystems (e.g. Lindenmayer *et al.*, 2008; Sheaves, 2009; Beger *et al.*, 2010a). This broad and flexible definition, together with the diversity and complexity of approaches for its quantification, makes connectivity difficult to conceptualize and evaluate (Calabrese & Fagan, 2004). We focus on habitat connectivity or the connectedness of patches of biogenic structure (in this case coral reef and mangroves) for particular mobile taxa (Lindenmayer & Fischer, 2007). The effects of similar habitat connections can be seen in, and among, marine, freshwater and terrestrial ecosystems (Beger *et al.*, 2010a). The benefits of this connectivity have, however, been degraded through habitat loss and alteration and species exploitation. Given the impending impacts of climate change, and the dearth of empirical evidence, a better understanding of the role for habitat connectivity in conservation is required (Estes *et al.*, 2011).

Habitat connectivity has recently been shown to improve the effectiveness of marine reserves in the back-reef seascapes of the tropical Caribbean Sea (Nagelkerken *et al.*, 2012) and subtropical Pacific Ocean (Olds *et al.*, 2012a). These seascapes support a heterogeneous mix of coral reef, mangrove, seagrass and soft sediment habitats and are linked by an array of biological, physical and chemical processes (Grober-Dunsmore *et al.*, 2009). Fish, for example, migrate among habitats to utilize different resources (Nagelkerken, 2009), and populations and assemblages are influenced by the availability and spatial arrangement of habitats across the seascape (reviewed by Grober-Dunsmore *et al.*, 2009; Boström *et al.*, 2011; Berkström *et al.*, 2012). These seascape effects can also drive a range of ecological processes and functions, namely: herbivory (e.g. Mumby & Hastings, 2008), predation and predator–prey behaviour (e.g. Sheaves, 2009), food web structure (e.g. Heck *et al.*, 2008) and ecological resilience (e.g. Olds *et al.*, 2012b). Consequently, seascapes with well-connected habitats may support different assemblages and

operate under different regimes of process and function than those that are isolated (*sensu* Nyström & Folke, 2001).

We examined connectivity between mangroves and adjacent coral reefs, which are functionally linked by fish during tidal and diel movements and by ontogenetic migrations from juvenile nurseries to adult habitats (Nagelkerken, 2009; Sheaves, 2009). These connections operate across a range of scales, from 100 s of metres for local feeding movements (e.g. Boström *et al.*, 2011) to 10 s of kilometres for ontogenetic habitat shifts (Mumby, 2006). They can affect fish biomass in both habitats (Mumby *et al.*, 2004), and the influence of marine reserves on fish populations (Olds *et al.*, 2012a) and ecological resilience (Olds *et al.*, 2012b). The importance of this habitat connectivity to the effectiveness of marine reserves was evaluated across the three regions of the western Pacific Ocean: Roviana Lagoon (Solomon Islands), the Palm Islands (Great Barrier Reef, Australia) and Moreton Bay (Australia). These regions are separated by up to 20° of latitude and vary in seascape heterogeneity, tidal regimes and reserve management styles. Each contains effective no-take marine reserves (e.g. Williamson *et al.*, 2004; Aswani *et al.*, 2007; Olds *et al.*, 2012a) in heterogeneous seascapes with fish assemblages that are influenced by habitat connectivity and seascape ecology (e.g. Aswani & Hamilton, 2004; Mellin *et al.*, 2010; Olds *et al.*, 2012c). The benefits of marine reserves (e.g. Edgar *et al.*, 2011) and the importance of seascape ecology to fish assemblages (e.g. Mellin *et al.*, 2010) have been demonstrated across similar regional scales, however, to date, their potential interactive effects have only been examined at local scales. We tested the broader applicability of the hypothesis that mangrove-reef connectivity could promote the ability of reserves to enhance fish abundance, which had been established at a local scale (10 s of km) (Olds *et al.*, 2012a) by examining the interaction of these factors across 2000 kilometres of the western Pacific Ocean. Given that mangroves provide a nursery for many juvenile reef fish, and therefore often harbour smaller individuals, a greater effect of marine reserves was anticipated on fish in adjacent reef habitat. Marine reserve effects vary with reserve age, context, latitude and the intensity of illegal fishing effort (e.g. Lester *et al.*, 2009). The influence of habitat connectivity also differs with variation in seascape composition, heterogeneity, latitude and tidal range (e.g. Nagelkerken, 2009). Consequently, we also examined whether the magnitude of reserve-connectivity effects was explained by variation in seascape heterogeneity, reserve size and age, latitude and tidal regime.

MATERIAL AND METHODS

Seascapes studied

We surveyed the fish of coral reef and mangrove habitats in marine reserves and unprotected control locations in Roviana Lagoon, the Palm Islands and Moreton Bay (Fig. 1). These locations were selected to provide for variation along gradients of reserve size, seascape heterogeneity, mangrove inundation frequency and latitude. Roviana Lagoon (8°17' S, 157°25' E) is located in the Solomon Islands and is part of the Coral Triangle

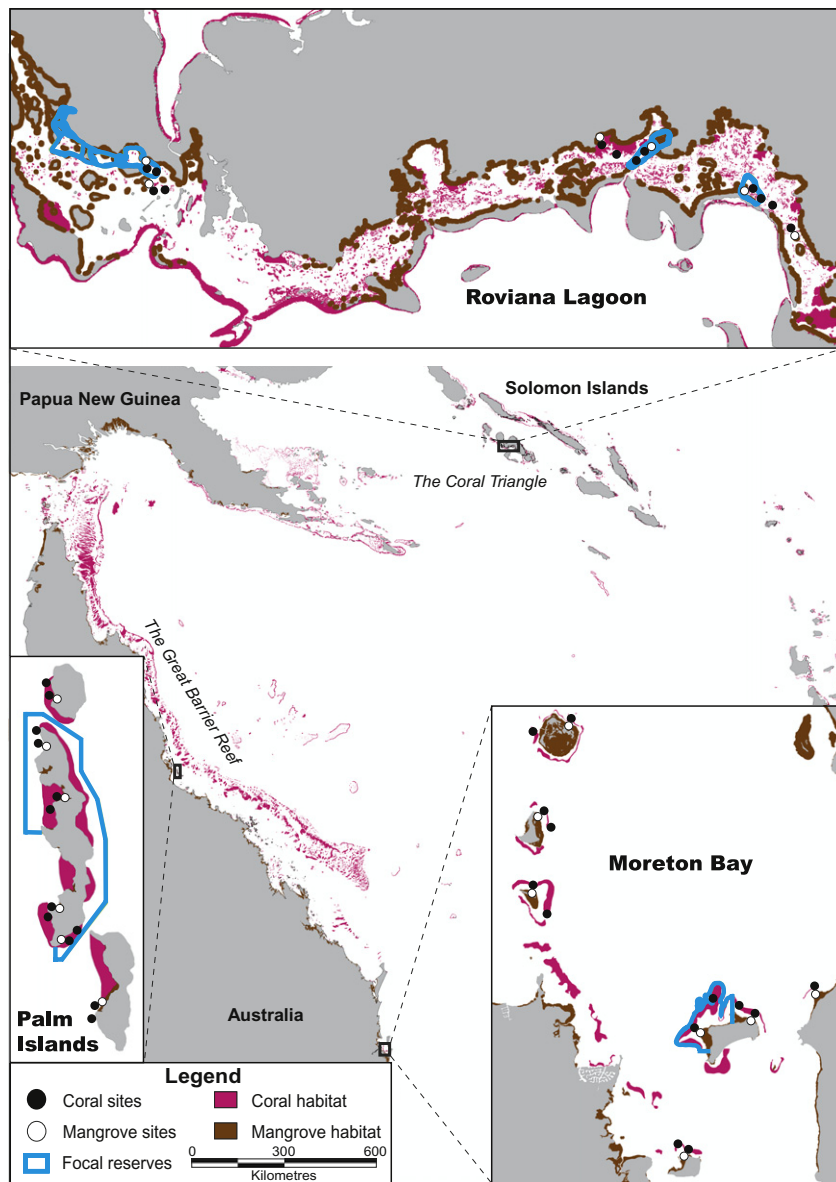


Figure 1 Mangrove and coral reef habitats of Roviana Lagoon (Solomon Islands), the Palm Islands (Great Barrier Reef) and Moreton Bay (Australia). Survey sites depicted as circles over mangrove and coral reef habitat.

eco-region, which is recognized as the global centre of marine biodiversity with the highest priority for conservation (Veron *et al.*, 2009). The lagoon is formed by raised offshore coral islands and supports heterogeneous tropical reef seascapes, which are managed in a network of small community-based marine reserves (established in 1999 and managed by the Roviana Conservation Foundation) (Aswani *et al.*, 2007). The Palm Islands (18°35' S, 146°30' E) are located on the inner Great Barrier Reef (GBR), Australia, a World Heritage Area of globally significant biodiversity and the world's largest marine reserve network (McCook *et al.*, 2010). The island group contains 10 granite-based continental islands, which are fringed by extensive shallow coral reefs and support stands of clear-water mangroves along their western shorelines (Williamson *et al.*, 2004; Barnes *et al.*, 2012). These tropical reef scapes are managed in the Great Barrier Reef Marine Park (established in 1987 and managed by the Great Barrier Reef Marine Park Authority) (McCook *et al.*,

2010). Moreton Bay (27°15' S, 153°15' E), Australia, is a subtropical embayment south of the GBR that has been proposed as a potential refuge for tropical reef species threatened by climate change (Lybolt *et al.*, 2011). It supports marginal fringing coral reefs, mangroves and seagrass in a heterogeneous estuarine seascape, which is managed in the Moreton Bay Marine Park (established in 1997 and managed by the Queensland Parks and Wildlife Service) (Olds *et al.*, 2012a). At the time of assessment, marine reserves had been closed to harvesting for 8 years in Roviana Lagoon, 24 years in the Palm Islands and 13 years in Moreton Bay.

Spatial analysis

Field expeditions to Roviana Lagoon, the Palm Islands and Moreton Bay were undertaken between December 2009 and October 2011. We surveyed fish assemblages in three marine

reserves and three unprotected control locations in Roviana Lagoon and the Palm Islands, and in one marine reserve and six unprotected locations in Moreton Bay. At the time of survey, there was only one effective marine reserve protecting back-reef seascapes in Moreton Bay. We adopted the most powerful experimental design possible in this circumstance, and utilized asymmetrical analyses to examine whether the single reserve location behaved differently to the average of multiple controls (see Olds *et al.*, 2012a). At each location, we examined fish assemblages in mangroves close to reefs, on reefs close to mangroves and on reefs distant from mangroves (Fig. 1). This design was adopted to capture the effects of tidal and ontogenetic connectivity between mangroves and reefs on fish assemblages and, therefore, necessitated spatial structure to the arrangement of sampling sites. Habitat connectivity was quantified as the edge-to-edge isolation distance between habitats from existing benthic habitat maps using ArcGIS (ESRI, Redlands, CA, USA) (sources: Great Barrier Reef Marine Park Authority, Queensland Department of Environment and Resource Management, Roviana Conservation Foundation and United Nations Environment Program). Isolation distances were scaled to the daily home ranges of species common to the coral reef and mangrove habitats of the western Pacific (*sensu* Grober-Dunsmore *et al.*, 2009). Close reefs were within 250 m of mangroves, and isolated reefs were at least 500 m from mangroves. This scale encompassed daily home ranges of adult snappers (Lutjanidae), groupers (Serranidae), rabbitfish (Siganidae) and bream (Sparidae) (e.g. Sheaves, 1993; Zeller *et al.*, 2003; Meynecke *et al.*, 2008; Fox & Bellwood, 2011). Ideally, home ranges of other species would also be included when selecting a spatial context, but movement data are lacking for other fish families in the region. Studies of spatial patterns in ecology can only infer causality after first falsifying potential alternative explanations (Mumby *et al.*, 2004), and we verified that reef fish distributions were not explained by covariation of habitat area, composition or benthic complexity and that illegal fishing effort did not vary with isolation or reserve status (see Appendix S1).

Fish assemblages

Fish assemblages on coral reefs and at the mangrove fringe were surveyed using underwater visual census (following Olds *et al.*, 2012a). Five replicate 50 × 4 m belt transects were censused at each site; reefs were surveyed at low tide when mangroves were dry and not accessible to fish, and mangroves were surveyed at high tide when they were inundated and accessible. Transects were standardized for depth, positioned in series parallel to the reef slope or mangrove fringe, and separated by a minimum of 50 m. Each census consisted of a diver swimming the transect and recording the species, size and abundance of all fish greater than 5 cm total length (TL).

Fish assemblages occurring in reef and mangrove habitats were organized into the following groups: harvested species, functional groups (i.e. herbivores, piscivores, benthic invertebrate feeders), families and densities of selected individual species. Species richness was also calculated as a surrogate for

functional diversity (Micheli & Halpern, 2005). Harvested species are most likely to respond to ecosystem protection; we used those listed as exploited in Australian fisheries (Rees *et al.*, 2012) and those exploited in the subsistence fisheries of Roviana Lagoon (e.g. Aswani & Hamilton, 2004). Herbivores are a crucial functional group underpinning reef resilience by grazing on algae (Hughes *et al.*, 2010); herbivore density was calculated from the families Acanthuridae, Ehippidae, Kyphosidae, Pomacanthidae, Scaridae and Siganidae (following Choat *et al.*, 2002). Piscivores are important in structuring marine food webs and influence trophic transfers among habitats (Sheaves, 2009); piscivore density was determined from species that commonly consume fish (following, Baker & Sheaves, 2005). Roving benthic invertebrate feeders undertake tidal or diel migrations to forage in habitats adjacent to coral reefs and can provide important subsidies to reef food webs when they return (Heck *et al.*, 2008); the density of benthic invertebrate feeders was calculated from the families Haemulidae, Holocentridae, Labridae, Lethrinidae, Mullidae and Nemipteridae. Harvested fish include species of herbivores, piscivores and benthic invertebrate feeders, whereas these trophic guilds are independent.

Data analysis

Reserve and habitat connectivity effects were evaluated using a modified control–impact design. Analysis examined effects on fish variables through comparison of reserve and control locations in each region separately: three reserves and controls from Roviana Lagoon and the Palm Islands and one reserve and six controls from Moreton Bay. Fish density data were log transformed to produce homogenous variances and analysed with analysis of variance (ANOVA). We used three-factor ANOVAs for reef fish and two-factor analyses for mangrove fish data from Roviana Lagoon and the Palm Islands. The factors were: protection (a fixed orthogonal factor), location (a random orthogonal factor) and habitat connectivity (a fixed orthogonal factor used in reef analyses only). Asymmetrical ANOVA (Underwood, 1992) was conducted for Moreton Bay, to examine whether the single reserve location differed from the average of the six controls (see Olds *et al.*, 2012a). We conducted two-factor ANOVAs for reef fish and one-factor analyses for mangrove fish. The factors were: location (an asymmetrical random orthogonal factor with only one reserve) and habitat connectivity (a fixed orthogonal factor used in reef analyses only). Post hoc Student–Newman–Keuls tests were used to differentiate significant means.

To determine if reserves and habitat connectivity influenced the composition of reef fish assemblages, data from each region were examined separately using permutational multivariate analysis of variance (PERMANOVA). Canonical analysis of principal coordinates (CAP) was used to visualize significant factors following PERMANOVA and to identify species that were primarily responsible for driving these differences (full description in Appendix S2).

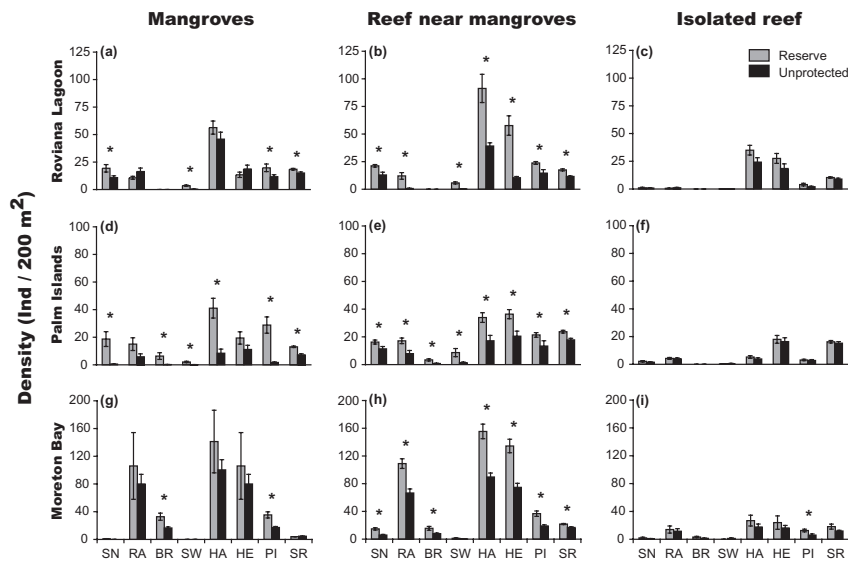


Figure 2 Density of snappers (Lutjanidae), rabbitfish (Siganidae), bream (Sparidae), sweetlip (Haemulidae), harvested fish, herbivores, piscivores and species richness in mangroves and on coral reefs (mean \pm SE). SN, snappers; RA, rabbitfish; BR, bream; SW, sweetlip; HA, harvested fish; HE, herbivores; PI, piscivores; SR, species richness. *Represent significant differences between reserve and unprotected locations (identified by Student–Newman–Keuls post hoc analyses).

The influence of marine reserves on fish abundance varies with reserve age and the intensity of illegal fishing effort (e.g. Lester *et al.*, 2009). Similarly, the effects of habitat connectivity potentially also differ with variation in seascape composition, heterogeneity, latitude and tidal range (Nagelkerken, 2009). Thus, we used general linear models (GLM) to examine the effect of these reserve and seascape variables on the magnitude of reserve-connectivity effects among the seven reserves surveyed. Magnitude of effect was expressed as the proportion of all reef fish species for which abundance was positively affected by a statistically significant interaction between reserve and habitat connectivity effects. Reserve variables included: reserve area, age and intensity of illegal fishing effort (refer Appendix S1). Seascape variables included: habitat area (proportion of each reserve containing mangroves and coral reef), duration of mangrove inundation (hours each day), latitude and the distance to rivers and oceanic passages. Analyses were conducted separately for each independent variable. We used an arcsine square root transformation on the index of reserve-connectivity effects (i.e. the proportion of all reef fish species affected) to meet the assumptions of homogeneity of variance for the GLM.

RESULTS

Habitat connectivity and reserve effects on fish assemblages

Protection had the greatest effect on fish densities on reefs close to mangroves. Snappers (Lutjanidae) and rabbitfish (Siganidae) were more abundant on reserve reefs close to mangroves in all three regions (Fig. 2, Appendix S3). Harvested fish, herbivores and species richness followed the same trend at all locations, except one protected area in Roviana Lagoon (Fig. 2, Appendix S3). Sweetlip (Haemulidae) and piscivores were more abundant on reserve reefs close to mangroves in Roviana Lagoon and the

Palm Islands (Fig. 2, Appendix S3). Piscivores were more abundant on reserve reefs in Moreton Bay, regardless of their isolation from mangroves (Fig. 2, Appendix S3). Bream (Sparidae) were also more abundant on reserve reefs close to mangroves in the Palm Islands and Moreton Bay but were not recorded in Roviana Lagoon (Fig. 2, Appendix S3).

Protection also influenced fish densities in mangroves that were close to reefs. Piscivores were more abundant in reserve mangroves in all three regions (Fig. 2, Appendix S3). Snapper and sweetlip were more abundant in reserve mangroves in Roviana Lagoon and the Palm Islands (Fig. 2, Appendix S3); species richness also followed this trend. Bream were more abundant in reserve mangroves in the Palm Islands and Moreton Bay but were not recorded in Roviana Lagoon (Fig. 2, Appendix S3). Harvested species were more abundant in protected mangroves in the Palm Islands; effects elsewhere varied among locations (Fig. 2, Appendix S3). There was no consistent effect of protection on the abundance of herbivores or rabbitfish in mangroves (Fig. 2, Appendix S3).

Habitat connectivity influenced the effects of marine reserves on the abundance of 14 fish species, which utilized adjacent reefs and mangroves (Appendix S3). This included four snappers, three rabbitfish, two sweetlip and two bream, which were largely responsible for observed patterns in family and functional group abundance. It also incorporated one hardyhead (Atherinidae), an emperor (Lethrinidae) and a parrotfish (Scaridae). The magnitude of these species-level effects, however, differed among regions with variation in species composition and abundance.

The effects of habitat connectivity on reef fish assemblages were influenced by an interaction with reserve status in Roviana Lagoon, the Palm Islands and Moreton Bay (Fig. 3, Appendix S2). These differences were driven by variation in the abundance of bream (Sparidae), rabbitfish (Siganidae), snappers (Lutjanidae) and sweetlip (Haemulidae), but the species responsible differed among regions (Fig. 3, Appendix S2).

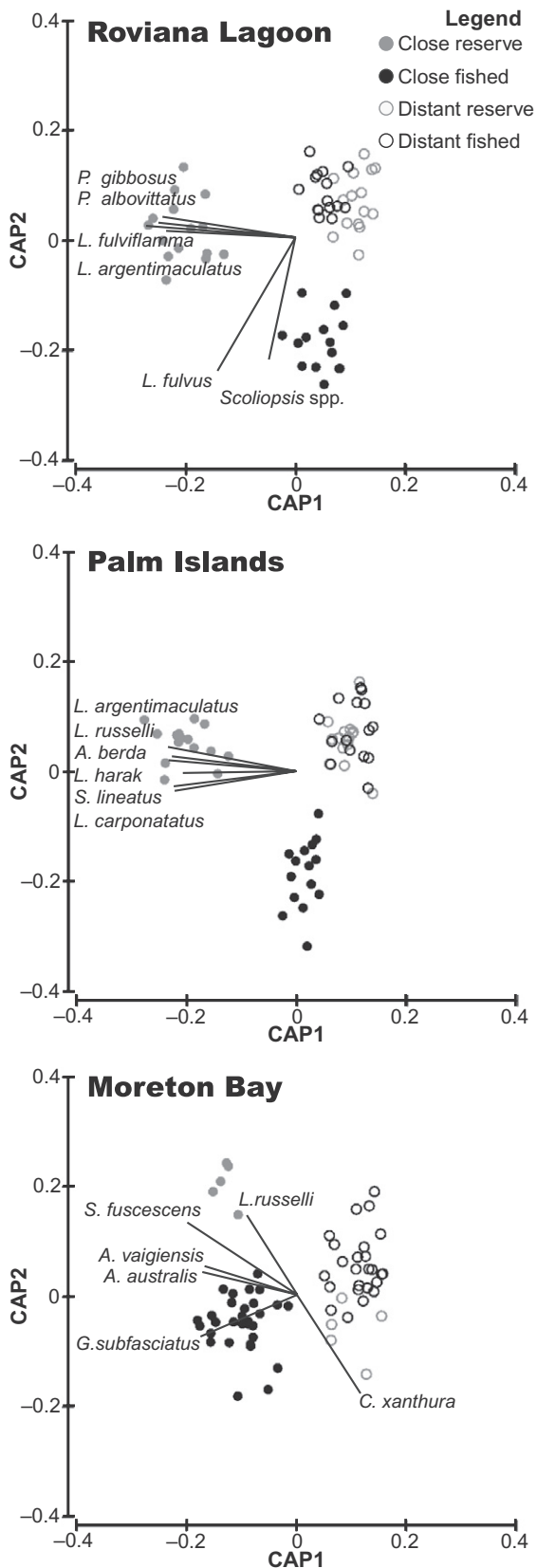


Figure 3 Constrained canonical analyses of principal coordinates (CAP) illustrating relationships among reef fish assemblages in Roviana Lagoon ($\mathcal{D}^2 = 0.84$, $m = 6$, $LoA = 83.33\%$), the Palm Islands ($\mathcal{D}^2 = 0.88$, $m = 12$, $LoA = 78.33\%$) and Moreton Bay ($\mathcal{D}^2 = 0.89$, $m = 10$, $LoA = 92.31\%$). Ordinations based on modified Gower (Log 2) dissimilarities with Status (black versus grey circles) and Connectivity (shaded versus unshaded circles). Species correlations with the canonical axis are represented as vectors for species with Pearson R -value greater than 0.6; e.g. *Lutjanus argentimaculatus* is positively correlated with protected sites near mangroves in Roviana Lagoon and the Palm Islands.

Spatial variation in the magnitude of reserve-connectivity effects

Of the eight reserve and seascape variables examined in the GLMs, only the area of mangroves and reef ($r^2 = 0.80$, $P = 0.041$), mangrove inundation ($r^2 = 0.81$, $P = 0.037$) and distance to nearest river ($r^2 = 0.86$, $P = 0.020$) were correlated with the magnitude of reserve-connectivity effects (Fig. 4, Appendix S4). Nonlinear, polynomial models for each of these three variables explained significant spatial variation in the magnitude of reserve-connectivity effects among reserves in Roviana Lagoon, the Palm Island group and Moreton Bay (Fig. 4, Appendix S4). The magnitude of reserve-connectivity effects increased with habitat area (i.e. proportion of each reserve containing mangroves and coral reef) and the duration of mangrove inundation (hours each day) and decreased with distance from the nearest river (Fig. 4). In contrast, the magnitude of reserve-connectivity effects was not correlated with spatial variation in reserve latitude, area or age, the distance to nearest oceanic passage, or the intensity of illegal fishing effort (Appendix S4).

DISCUSSION

Conservation actions are typically concerned with enhancing biodiversity and ecosystem resilience, and consequently, considerable research has focused on identifying important species, processes and landscape elements for conservation (Estes *et al.*, 2011). Connectivity is paramount among these, and consequently, is now being integrated into strategies for ecosystem-based management (e.g. Massol *et al.*, 2011) and spatial conservation planning (e.g. Foley *et al.*, 2010). This concept has been well researched in terrestrial ecosystems, but by comparison its value remains poorly understood for marine conservation and fisheries management (Lindenmayer *et al.*, 2008; Sheaves, 2009; Estes *et al.*, 2011). We demonstrate positive effects of habitat connectivity on the effectiveness of reserves across the western Pacific Ocean, and in doing so extend the findings of Olds *et al.* (2012a) from a local (10 s of km) to regional (over 2000 km and 20° of latitude) scale. Our results show that connectivity between reefs and mangroves (with a threshold at the 100–1000 m scale) can improve the effectiveness of reserves and increase the abundance of four fish families, harvested fish, herbivores and piscivores, and species richness on protected reefs. The broader implications of this result are,

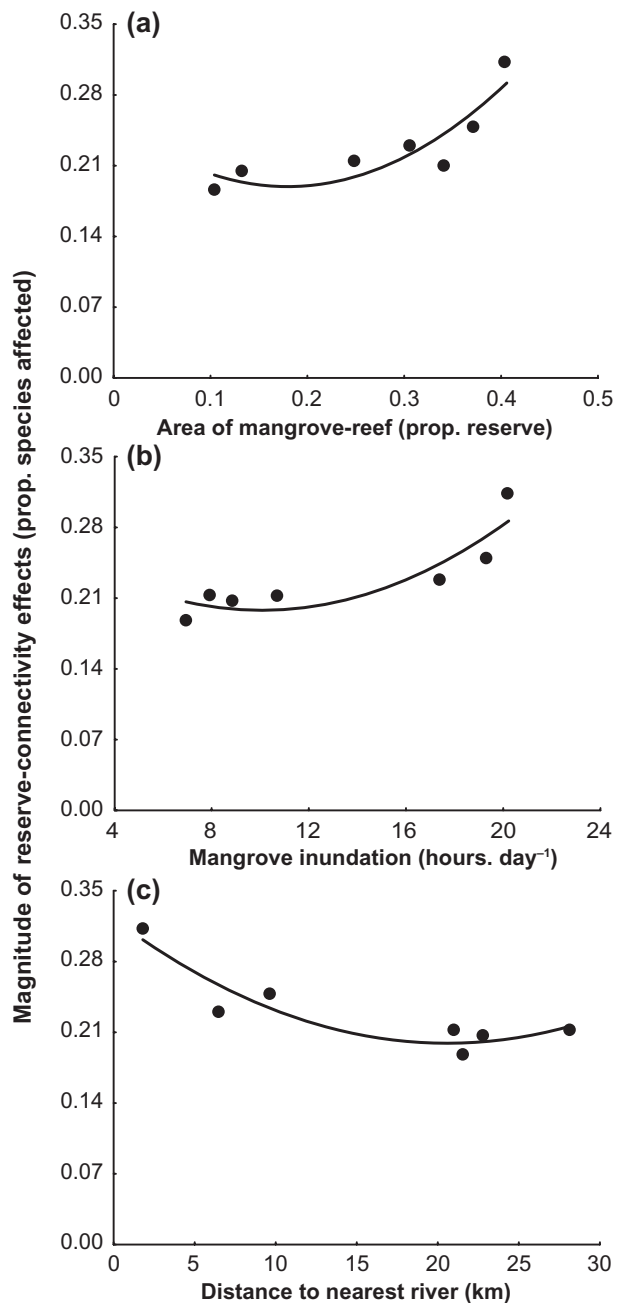


Figure 4 Relationships between the magnitude of reserve-connectivity effects (expressed as the proportion of reef fish species affected by a statistically significant interaction between reserve and connectivity effects) and: (a) area of mangrove and reef (i.e. proportion of each reserve containing mangroves and coral reef), (b) the duration of mangrove inundation (hours each day), and (c) the distance of reserves from the nearest river. Curves are lines of best fit from significant ($P < 0.05$) polynomial general linear models, as described in the text.

however, limited by the fact that we were unable to evaluate fish assemblages prior to reserve establishment. Prior data would be necessary to effectively control for natural spatial and temporal variability, but are commonly not available for studies of reserve

effectiveness (Lester *et al.*, 2009). Nevertheless, our results support greater incorporation of spatial ecology into ecosystem-based management (*sensu* Foley *et al.*, 2010; Massol *et al.*, 2011). It is important to recognize, however, that there can be many drawbacks to connectivity in reserve networks, including enhanced pathogen and invasive species exchange (Kellner & Hastings, 2009), reduced spatial risk spreading (McCook *et al.*, 2009), decreased ecological representation (Game *et al.*, 2008) and, for reefs nearer to mangroves, increased proximity to sources of sediments, nutrients and detritus (Beger *et al.*, 2010a). The decision to prioritize connectivity in conservation planning, therefore, creates a trade-off between these competing interests and other conservation targets (Hodgson *et al.*, 2009; Beger *et al.*, 2010b).

Our findings demonstrate that connectivity between reefs and mangroves can improve the effectiveness of marine reserves, but they also indicate that the magnitude of these reserve-connectivity effects can vary among different seascapes. By examining the potential drivers of this spatial variation (i.e. reserve and seascape influences), we determined that the relative magnitude of reserve-connectivity effects correlated with differences among reserves in the area of mangroves and reef, duration of mangrove inundation and distance to the nearest river. This result is not particularly surprising as these variables can affect the influence of habitat connectivity on coastal fish assemblages (e.g. Nagelkerken, 2009). It is noteworthy, however, that these seascape-level effects were more influential than other reserve-level attributes (i.e. age and intensity of illegal fishing effort), which also affect reserve performance (e.g. Lester *et al.*, 2009). These results suggest that greater effects of mangrove-reef connectivity might be expected for reserves in heterogeneous inshore seascapes, which lie close to rivers, and experience high frequencies of mangrove inundation. Collectively, these variables influence the area and availability of both habitats, and consequently exert indirect effects on habitat connectivity. Inter-reef connectivity is, perhaps, more important to the composition of reef fish assemblages on offshore reefs (*sensu* Mellin *et al.*, 2010), and the performance of reef reserve networks may similarly be enhanced by incorporating inter-reef connectivity (Beger *et al.*, 2010b) and ontogenetic linkages with nursery habitats (Nagelkerken *et al.*, 2012).

Mangroves and coral reefs are connected by the tidal, diel and ontogenetic migrations of a range of fish species (Nagelkerken, 2009; Sheaves, 2009). Mangroves are important juvenile habitats for many reef species, and consequently typically support smaller and younger individuals (Mumby *et al.*, 2004; Barnes *et al.*, 2012; Nagelkerken *et al.*, 2012). The effects of mangrove to reef ontogenetic habitat shifts may be apparent in the results of this study, and emphasized by the greater influence of marine reserves on species on coral reefs than in mangroves. This is an interesting idea, for it suggests that we may need to reconsider how reserve effects are evaluated in near-shore coastal habitats. Indeed, the value of juvenile habitats is accepted to result from their importance for maintaining a high density, survival, growth and productivity of juveniles, which underpins the biomass of adults in offshore habitats (*sensu* Beck *et al.*, 2001).

The nursery-reef transition zone, therefore, provides an important ecological corridor that needs further attention in spatial conservation planning, and the established framework for assessing nursery productivity may prove valuable for future reserve assessment (Nagelkerken *et al.*, 2012; Olds *et al.*, 2012a). The value of mangrove-reef connectivity is particularly well understood for reef fish assemblages in the Caribbean Sea and western Indian Ocean (reviewed by Grober-Dunsmore *et al.*, 2009; Boström *et al.*, 2011; Berkström *et al.*, 2012). Interestingly, our results suggest that connectivity between Pacific mangroves and reefs affects reef fish from the same families and functional groups, over similar scales (i.e. 100 s of metres), to those in the tropical Caribbean and Indian Ocean (e.g. Boström *et al.*, 2011, 2012). Links with neighbouring seagrass also influence the composition of fish assemblages in back-reef seascapes from each region (e.g. Olds *et al.*, 2012c). We suggest, therefore, that seascape connectivity is likely to enhance the effectiveness of marine reserves in similar heterogeneous tropical seascapes elsewhere (*sensu* Nagelkerken *et al.*, 2012). It is also important to emphasize that the effects of connectivity on reserves appeared to hold across a range of latitudes, from the highly diverse tropical Coral Triangle to marginal reef seascapes at the limits of their subtropical distribution. We therefore recommend that heterogeneous landscapes with high habitat connectivity should be viewed as priorities for the conservation of exploited consumers and the maintenance of ecological processes. The specific approach for evaluating and incorporating habitat connectivity into spatial conservation planning will, however, vary out of necessity with the mobility of organisms and the spatial heterogeneity of the ecosystem of interest.

Our findings demonstrate positive effects of habitat connectivity on the effectiveness of reserves across the western Pacific Ocean. We show that connected reefs and mangroves in reserves support greater fish abundance and species richness than similar fished seascapes. Our results indicate that greater effects of mangrove-reef connectivity might be expected for reserves in heterogeneous inshore seascapes, whereas inter-reef connectivity is likely to be more important to the effectiveness of reserves on offshore reefs. We suggest that by explicitly incorporating connectivity into conservation planning, we may have better success in preserving biodiversity and maintaining healthy, functioning ecosystems.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Testing potential alternative explanations.

Appendix S2 Connectivity and reserve effects on fish assemblages.

Appendix S3 Connectivity and reserve effects on fish abundance.

Appendix S4 Spatial variation in magnitude of reserve-connectivity effects.

BIOSKETCH

Andrew Olds is a research fellow at Griffith University and the Australian Rivers Institute – Coast and Estuaries (Gold Coast, Australia). His research focuses on community ecology, biogeography and the impacts of global change on marine ecosystems.

The research team includes ecologists from universities and research organizations in Australia and Solomon Islands who are examining effects of marine reserves on ecological processes, ecosystem services and socioecological resilience. A.O., K.P and R.C. conceived and designed the study; A.O., P.M and S.A. collected the data; A.O. led the data analysis and writing; all authors contributed to interpreting the results and developing the manuscript.

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