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RESEARCH REVIEW

Quantifying the conservation value of seascape connectivity: a global synthesis

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ABSTRACT

Aim Connectivity structures populations, communities and ecosystems in the sea. The extent of connectivity is, therefore, predicted to also influence the outcomes of conservation initiatives, such as marine reserves. Here we review the published evidence about how important seascape connectivity (i.e. landscape connectivity in the sea) is for marine conservation outcomes.

Location Global.

Methods We analysed the global literature on the effects of seascape connectivity on reserve performance.

Results In the majority of cases, greater seascape connectivity inside reserves translates into better conservation outcomes (i.e. enhanced productivity and diversity). Research on reserve performance is, however, most often conducted separately from research on connectivity, resulting in few studies (< 5% of all studies of seascape connectivity) that have quantified how connectivity modifies reserve effects on populations, assemblages or ecosystem functioning in seascapes. Nevertheless, evidence for positive effects of connectivity on reserve performance is geographically widespread, encompassing studies in the Caribbean Sea, Florida Keys and western Pacific Ocean.

Main conclusions Given that research rarely connects the effects of connectivity and reserves, our thesis is that stronger linkages between landscape ecology and marine spatial planning are likely to improve conservation outcomes in the sea. The key science challenge is to identify the full range of ecological functions that are modulated by connectivity and the spatial scale over which these functions enhance conservation outcomes.

Keywords

Conservation planning, ecological processes, ecosystem functioning, landscape ecology, marine reserves.

INTRODUCTION

> *We are like islands in the sea, separate on the surface but connected in the deep.*
>
> William James

Movements of organisms, matter and energy are key ecological processes, connecting populations, habitats, food webs and ecosystems (Massol *et al.*, 2011; Hyndes *et al.*, 2014). This connectivity is also central to understanding population viability and the resilience of ecosystems to disturbance (Bernhardt & Leslie, 2013; Magris *et al.*, 2014). The fundamental importance of these linkages has long been recognized (Odum, 1968), and in recent years connectivity has become an increasingly important consideration in spatial conservation planning, complementing the long-standing focus on species persistence, habitat quality and area (Moilanen *et al.*, 2009; Hodgson *et al.*, 2011; Kool *et al.*, 2013). Examples of an increasing integration of connectivity in conservation include: optimizing the placement of reserves and the spacing of reserve networks; identifying and protecting key corridors of animal migration; limiting the spread of invasive species; and promoting the restoration of fragmented landscapes (Rudnick *et al.*, 2012; Green *et al.*, 2014).

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In the sea, as on land, the area, quality and spatial arrangement of habitats are key determinants of the distribution, movement, growth and survival of organisms (Irlandi & Crawford, 1997; Micheli & Peterson, 1999). Physical linkages between discontinuous habitats (either of the same or of different types) of the seafloor represent seascape connectivity (i.e. landscape connectivity in the sea); this connectivity can be quantified as functional connectivity (i.e. documented movement of organisms among patches or habitats) or structural connectivity (i.e. distribution of organisms or processes in relation to the spatial configuration of patches or habitats) (Grober-Dunsmore *et al.*, 2009). The importance of seascape connectivity has been well documented for post-settlement fish and crustaceans (i.e. individuals that have successfully recruited to a habitat or assemblage), which move among different habitats to spawn, forage or undertake ontogenetic habitat shifts (Pittman & McAlpine, 2003; Sheaves, 2009; Boström *et al.*, 2011). Moreover, seascape connectivity influences the spatial distribution of fish populations and fisheries catches and the outcomes of conservation initiatives (Nagelkerken *et al.*, 2012; Olds *et al.*, 2013).

Although connectivity is now a key consideration for marine conservation planning (Green *et al.*, 2014; Magris *et al.*, 2014), few studies actually provide empirical data about the conservation benefits of connectivity in marine ecosystems. There is a new urgency to address this knowledge gap because human activity has altered the condition of, and level of connectivity among, coastal populations, habitats and ecosystems (Boström *et al.*, 2011; Hyndes *et al.*, 2014; Nagelkerken *et al.*, 2015). For example, wetlands are being increasingly fragmented by coastal development, and the physical complexity of coral reefs is being eroded at a global scale with unanticipated consequences for connectivity, ecological resilience and provisioning of ecosystem services (Unsworth & Cullen, 2010; Rogers *et al.*, 2014). Furthermore, overharvesting of mobile consumers (e.g. fish, crustaceans) and the construction of barriers (e.g. dams, weirs, levees, sea walls) to animal migration has also physically degraded key connectivity pathways, affecting food webs, assemblage composition, population viability and the condition of marine ecosystems (Fig. 1) (Valentine *et al.*, 2008; Nagelkerken *et al.*, 2015).

General concepts and paradigms in seascape ecology and connectivity have been reviewed elsewhere (e.g. Grober-Dunsmore *et al.*, 2009; Boström *et al.*, 2011; Pittman & Olds, 2015), but no synopsis exists that explicitly addresses the question of whether and how connectivity enhances the effectiveness of marine reserves. Here we review studies of seascape connectivity (i.e. connectivity among habitats in seascapes) or habitat connectivity (i.e. connectivity among patches of the same habitat), focusing on post-settlement fish and crustaceans, to assess whether greater connectivity translates into consistently better conservation outcomes for populations, assemblages or ecosystem functioning for reserves. Our review examines connectivity in seascapes that lie within reserves and span reserve boundaries. Fish and crustaceans move among habitats in seascapes, are commonly managed using reserves and are, therefore, ideal model organisms for examining the role of connectivity in con-

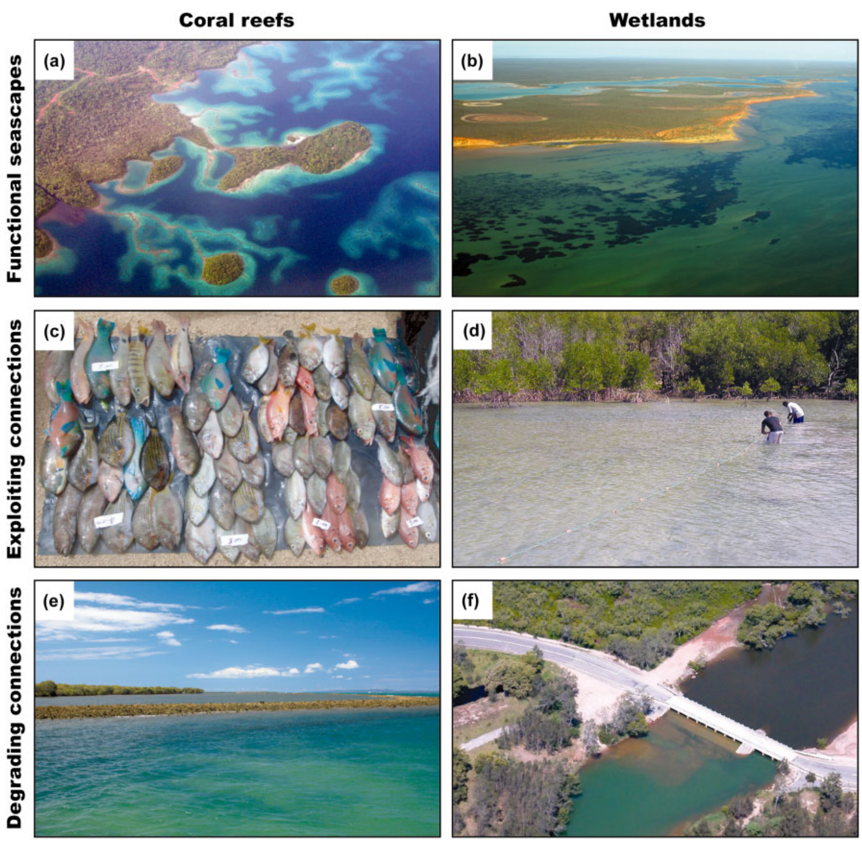

Figure 1 Common seascapes and impacts on connectivity in marine ecosystems (coral reefs, left; estuarine wetlands, right). We illustrate three types of connectivity: (1) largely unmodified seascapes with intact connections (a, b), (2) connections that are exploited to harvest organisms as they move regularly across seascapes (c, d), and (3) human alterations of connections illustrated by engineering structures (levees, weirs) that impede movement (e, f). Photographs by A.D.O., P.S.M., S.A. in Australia (b, e, f), Papua New Guinea (d), and Solomon Islands (a, c).

servation. We discuss implications for spatial conservation planning and we identify important knowledge gaps to be targeted in future research.

Our focus in this review is on connectivity of organisms post-settlement in reef and wetland seascapes, but the concepts and approach that we address are relevant to other seascapes. Pre-settlement processes (i.e. larval dispersal, population connectivity) are also an important consideration in marine spatial planning (e.g. facilitating network connectivity), but the potential role of larval dispersal for marine conservation has been reviewed widely (Cowen & Sponaugle, 2009; Green *et al.*, 2014; Jones, 2015). To determine the conservation value of seascape connectivity we have therefore focused on studies that have examined these effects for adult and juvenile animals.

SEASCAPE CONNECTIVITY AND MARINE CONSERVATION

Connectivity is important for conservation, mainly because populations of mobile organisms are spatially linked and adjacent ecosystems can function as linked units forming a habitat mosaic (Massol *et al.*, 2011; Green *et al.*, 2014). Connectivity can enhance the performance of individual marine reserves (Olds *et al.*, 2014) and mechanistically links habitat patches in reserves with those in other reserves, or in adjacent fished waters (Pittman *et al.*, 2014). Connectivity influences the number of organisms exported from reserves (both adults and larvae) to replenish populations in fished waters (i.e. spillover) and links populations among reserves (e.g. Freeman *et al.*, 2009; Halpern *et al.*, 2009; Harrison *et al.*, 2012). For example, spillover of fish from reserves is likely to be greatest where reserves are surrounded by contiguous habitat that provides greater connectivity (Edgar *et al.*, 2014). This process can, however, also limit the recovery of fished populations within reserves (Babcock *et al.*, 2012). Seascape connectivity within reserves and reserve networks can also promote ecosystem resilience and facilitate access to refugia (Bernhardt & Leslie, 2013; Magris *et al.*, 2014). Better-connected populations and habitats in reserves can recover more quickly from disturbance through the arrival of individuals or propagules from other locations (i.e. recolonization effects) (Beger *et al.*, 2010; Green *et al.*, 2014) or via the ecological processes (e.g. herbivory) that mobile species provide for the functioning of ecosystems (Mumby, 2006; Olds *et al.*, 2012). Connectivity also enables organisms to access refugia in higher latitudes, or in deeper, cooler water, when moving away from the thermal impacts of climate change and, therefore, provides the mechanism for linking reserves across bioregions (Magris *et al.*, 2014).

Marine reserves provide model systems for investigating the ecological importance of connectivity for conservation. Marine reserves can have significant positive effects on the density, body size, biomass and demographic parameters of harvested fish and invertebrates (Lester *et al.*, 2009; MacNeil *et al.*, 2015), particularly when reserves prohibit fishing, are well enforced, old (> 10 years), large (> 100 km^2) and isolated by deep water or sand (Edgar *et al.*, 2014). Large consumer populations inside reserves can also affect the abundance and movement of competitors and prey species, and drive trophic cascades that structure the condition of benthic communities (Babcock *et al.*, 2010; MacNeil *et al.*, 2015). Furthermore, marine reserves can promote the transfer of carbon among ecosystems, linking ecological processes and food webs across seascapes (Langlois *et al.*, 2005; Salomon *et al.*, 2008). These effects on movement ecology and ecosystem functioning provide key mechanisms through which reserves influence connectivity (Valentine *et al.*, 2008; Olds *et al.*, 2012; Pittman *et al.*, 2014).

ECOLOGICAL STUDIES OF SEASCAPE CONNECTIVITY

To evaluate the importance of seascape connectivity in conservation we compiled a database of all peer-reviewed studies that reported effects of connectivity on marine fauna and ecological processes. The ISI Web of Knowledge database was searched using all permutations of the keywords: seascape, connectivity (connect*, link*, move*) and habitat (reef, kelp, mangrove, saltmarsh, seagrass, wetland). This database was then refined (using the keywords: MPA, no-take area, protected area, conservation area, reserve, spillover) to identify studies that examined connectivity effects in reserves, and those that directly quantified both connectivity and reserve effects. Connectivity studies focused on structural (i.e. distribution of organisms or processes) and functional (i.e. movement) measures (Grober-Dunsmore *et al.*, 2009). Reserve studies were categorized based on four common criteria for performance: 'production' (i.e. abundance, density, biomass), diversity (i.e. diversity, richness, composition), ecological processes (i.e. herbivory, predation, recruitment) and spillover (i.e. movement from inside to outside reserves) (Lester *et al.*, 2009).

We identified 213 studies that reported on connectivity, of which 143 were in coral and rocky reef seascapes and 70 in wetland systems (i.e. seagrass, mangrove and saltmarsh) (Fig. 2, Appendix). Most studies were from the Caribbean Sea (56), Australia (47), the Florida Keys (19), Tanzania (18), North America (15), the Mediterranean Sea (10), the Gulf of Mexico (8) and Indonesia (7), illustrating a concentration of research in tropical seascapes (Fig. 2, Appendix S1 in Supporting Information).

One fifth ($n = 45$) of studies that examined connectivity also addressed questions of marine reserve performance (Appendix S2). Most of these focused on structural (32) or functional (9) connectivity for fishes, whilst only four measured connectivity for crustaceans. All were conducted in reef seascapes (38 in coral reef and 7 in rocky reef systems), with most studies (35) examining the conservation benefits of seascape connectivity (i.e. linkages among different habitat types) and just a few (10) exploring the importance of habitat connectivity (i.e. linkages among patches of the same habitat type). There were no consistent differences in spatial scale between studies that examined seascape or habitat connectivity, or that focused on different types of organisms. Studies of functional connectivity were, however, generally conducted over a broader spatial scale (i.e.

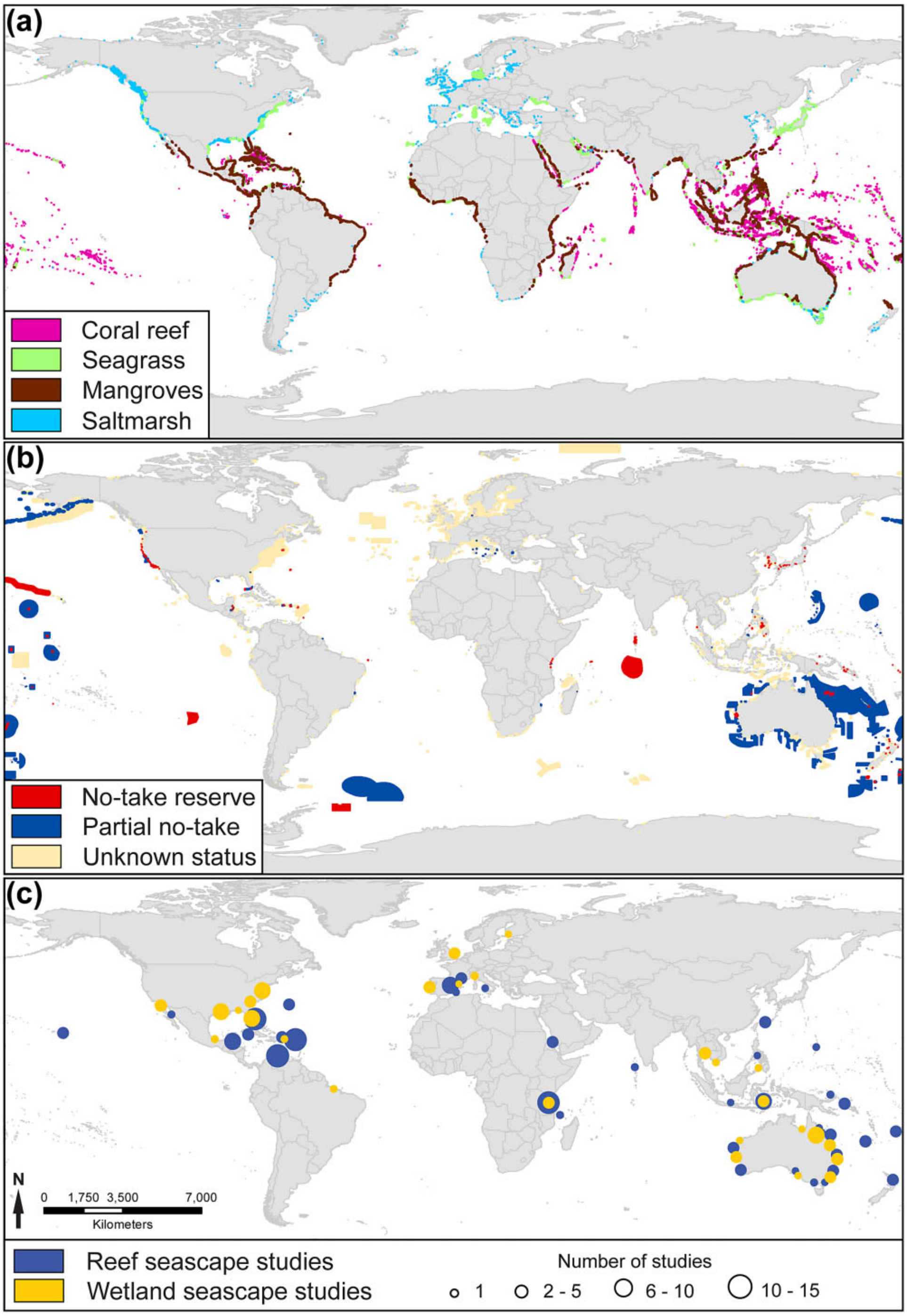

Figure 2 Global distribution of coral reef, seagrass, mangrove and saltmarsh ecosystems (a); marine reserves (i.e. no-take areas), marine parks (i.e. partial no-take areas) and other conservation areas (i.e. with unknown status) (b); and connectivity studies in reef and wetland seascapes (c) (Appendix). Information on the extent and geographic distribution of ecosystem types and marine conservation areas has been sourced from the United Nations Environment Programme World Conservation Monitoring Centre (UNEP-WCMC).

thousands to tens of thousands of metres) than studies of structural connectivity (i.e. hundreds to thousands of metres) (Appendix S2).

Twenty-seven studies examined connectivity effects inside reserves without explicitly testing reserve effectiveness ('connectivity effects inside reserves'). Eight studies quantified connectivity and reserve effects separately (i.e. they evaluated connectivity but did not examine whether it influenced reserve performance). Ten studies (i.e. fewer than 5% of seascape studies that examined connectivity) directly evaluated whether connectivity influenced reserve performance (Fig. 3, Appendix S2). These findings show that research on marine reserve perfor-

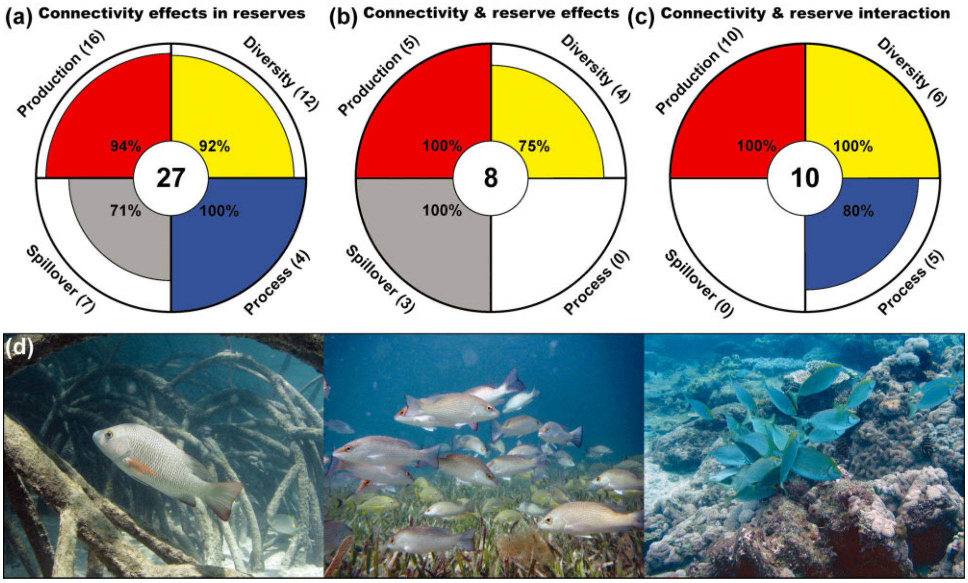

Figure 3 Connectivity effects contrasted between study types that incorporated the role of marine reserves to varying degrees: (a) studies that examined connectivity inside reserves but did not address reserve effects per se; (b) studies that quantified connectivity and reserve effects separately; and (c) studies that tested for an interaction between connectivity and reserve effects. Circle quarters represent summaries against reserve performance measures, with the number of studies of each type shown outside (in parentheses) and the total number of studies inside. The proportion of studies reporting significant effects is illustrated by a quadrant's size (and provided as percentages) (see Appendix S2). Panel (d) illustrates some of the principal attributes and mechanisms examined, such as the size and biomass of fish populations, the composition and diversity of assemblages and trophic interactions (e.g. herbivory). Photographs by A.D.O.

mance and seascape connectivity is typically conducted separately. This may suggest a separation (in terms of ecological theory or study design) between the disciplines of conservation biology and landscape ecology in many marine ecosystems. The 27 studies that examined connectivity inside reserves reported positive effects of greater connectivity on metrics that are commonly used to assess reserve performance, including: production (94% of studies), diversity (92%), ecological processes (100%) and spillover (71%) (Fig. 3, Appendix S2). The same was true for the eight studies that quantified connectivity and marine reserve effects separately, with 75–100% of these reporting positive effects of connectivity on the reserve performance measures production, diversity and spillover (Fig. 3, Appendix S2).

The most compelling result, however, is provided by studies that were designed specifically to test for interactive effects of seascape connectivity on reserve performance. Whilst comparatively under-represented with 10 out of 45 studies, 80–100% of these reported positive effects of greater connectivity on production (i.e. density or biomass), diversity (i.e. richness or composition) or ecological processes (i.e. herbivory, predation or recruitment) in reserves, compared with fished locations and reserves supporting isolated habitats (Fig. 3, Appendix S2). In the Caribbean Sea, for example, connectivity (quantified as habitat isolation and density at the scale of 200–1000 m) influenced marine reserve effects on fish biomass, species richness and assemblage composition on coral patch reefs at Glover's Atoll, Belize (Huntington *et al*., 2010). In the Florida Keys, connectivity (quantified as habitat isolation at the scale of 0–100 m) also influenced marine reserve effects on fish abundance and assemblage composition, as well as herbivory and predation rates, in seagrass meadows adjacent to coral reefs (Valentine *et al*., 2008). Similarly, in the western Pacific Ocean connectivity (quantified as habitat isolation at the scale of 100–1000 m) influenced marine reserve effects on fish abundance, species richness and assemblage composition on coral reefs, and in adjacent mangroves and seagrass (Olds *et al*., 2013). These seascape connectivity effects were largely driven by the distribution and behaviour of fish species that regularly use multiple habitats (or habitat patches) through their lives (e.g. fish from the families Haemulidae, Lethrinidae, Lutjanidae, Scaridae, Siganidae). Furthermore, the synergistic impact of reserves and connectivity on herbivorous fish (family Siganidae) also enhanced herbivory and coral recruitment on inshore coral reefs in Moreton Bay, eastern Australia (Olds *et al*., 2012). The results of studies that examined connectivity and reserve effects underscore the importance of cross-disciplinary integration of concepts and techniques to address new applied research questions at spatial scales that are operationally meaningful to conservation. We acknowledge that publication bias against neutral or insignificant results and our choice of search terms may have influenced the pool of literature reviewed (Babcock *et al*., 2010; Magris *et al*., 2014). These factors would, however, not detract from one of our main findings, namely that studies of reserve performance and seascape connectivity are often conducted separately.

INTEGRATING CONNECTIVITY INTO MARINE CONSERVATION

Based on the evidence available that strongly suggests a positive effect of greater connectivity on reserve performance, we recommend that seascape connectivity should be an important criterion in marine conservation. Four conditions will often have to be met when seeking to more comprehensively integrate connectivity in marine reserve design: (1) evaluate whether the benefits of connectivity result in a trade-off with other conservation considerations; (2) determine the spatial scales over which connectivity is likely to benefit reserve performance; (3) decide on a suitable approach for integrating connectivity into conservation planning and explicitly consider the effects of reserves on connectivity; and (4) quantify whether positive effects of connectivity for particular species (or groups of species) result in conservation benefits for the functioning of ecosystems, and vice versa.

Connectivity can have undesirable effects if it promotes the spread of invasive species, pathogens or pollutants (Rudnick *et al.*, 2012; Kool *et al.*, 2013). A stronger and more consistent emphasis on connectivity in conservation planning may also conflict with other socio-ecological considerations, including the representation of biodiversity, habitat area or quality (Beger *et al.*, 2010; Hodgson *et al.*, 2011), and the spatial spreading of risk to maximize population persistence and ecosystem resilience (Bernhardt & Leslie, 2013; Magris *et al.*, 2014). To be a clear priority for conservation, the potential benefits of connectivity must, therefore, exceed these risks and any potential costs to other conservation objectives.

Spatial scale is a key consideration for both marine conservation planning and seascape ecology (Magris *et al.*, 2014; Martin *et al.*, 2015). The synergistic effects of connectivity and reserves have typically (in six out of ten studies) been reported at the scale of hundreds to thousands of metres, which corresponds to tidal, daily and some ontogenetic fish movements (Boström *et al.*, 2011; Olds *et al.*, 2013), and is smaller than the size of most reserves (Lester *et al.*, 2009; Huijbers *et al.*, 2014). Within this range, the positive effects of connectivity will likely decline with distance, but the scale and shape of such effects may vary with the spatial extent of seascapes, the particular habitats these support and the mobility of the species of interest (*sensu* Olds *et al.*, 2013). The scale of any such decline-by-distance effect would also likely vary with the type of connectivity in question, with population connectivity (i.e. through larval dispersal and genetic exchange) occurring among habitat patches that are separated by much greater distances (i.e. tens to hundreds of kilometres) (e.g. Harrison *et al.*, 2012) than examined here. Studies are needed to identify factors that determine the scale over which connectivity effects reserve performance (priority questions 1 and 2, Table 1).

The identification of seascapes with optimal connectivity for maintaining biodiversity, productivity and ecosystem functioning is now a major goal in applied marine ecology (Pittman *et al.*, 2014; Nagelkerken *et al.*, 2015). With quantitative data on the scale of connectivity effects in seascapes, and the mode by which these affect reserve performance, seascape connectivity can be integrated into conservation by modifying reserve selection algorithms to incorporate connectivity (Moilanen *et al.*, 2009). Decision support tools (e.g. Marxan or Zonation) already provide some options for incorporating connectivity into conservation, and can be refined through further integration of quantitative data on connectivity (Beger *et al.*, 2010; Magris *et al.*, 2014). Given the potential for high spatial variability in connectivity effects, this may be achieved by prioritizing the conservation of seascapes that contain large, high-quality patches of multiple habitats (e.g. coral reefs and mangroves) within the spatial extent of species dispersal capabilities (i.e. home ranges, ontogenetic habitat shifts, pelagic larval duration) (e.g. Beger *et al.*, 2010; Edwards *et al.*, 2010; Nagelkerken *et al.*, 2015). This approach will have important consequences for how we rank the conservation of different marine habitats. In tropical seascapes, for example, mangroves, seagrasses and sandy shorelines are typically under-represented in marine conservation networks (relative to coral reefs) (Mumby, 2006; Unsworth & Cullen, 2010; Nagelkerken *et al.*, 2015). This integrates well with the gradual conceptual shift in perspective for marine conservation, from a historical focus on individual patches or habitats (Boström *et al.*, 2011) to the broader consideration of whole ecosystems transferring concepts and techniques from terrestrial landscape ecology.

A stronger focus on connectivity in conservation will likely benefit more than just fish populations and the performance of

Table 1 Priority questions for research on connectivity and conservation in marine ecosystems. Cited studies provide examples of potential approaches for examining each priority question.

Priority research questions
1. In situations where positive effects of connectivity on reserve performance are evident, what is the shape of the 'distance–decline' response curve and are thresholds evident in the effect of connectivity (e.g. Martin *et al.*, 2015)?
2. What factors are most important in determining the scale of connectivity effects on reserve performance (e.g. species biology, seascape composition, habitat quality, fishing pressure) (e.g. Olds *et al.*, 2013)?
3. Does connectivity improve reserve performance in seascapes that do not include coral reefs (e.g. estuaries, rocky reefs, sandy beaches, seamounts) (e.g. Langlois *et al.*, 2005)?
4. Does connectivity improve reserve performance for organisms other than fishes (e.g. MacArthur *et al.*, 2011)?
5. How widespread and prominent are connectivity effects on ecological processes (e.g. herbivory, predation, recruitment) in reserves (e.g. Valentine *et al.*, 2008)?
6. Do the effects of connectivity on ecological functions improve the resistance of protected ecosystems to disturbance, or influence their recovery (e.g. Olds *et al.*, 2012)?
7. To what extent do the characteristics of seascapes at reserve boundaries influence movement within reserves and spillover from reserves (e.g. Pittman *et al.*, 2014)?

marine reserves. It may, for example, also enhance the joint capacity of adjacent habitats, such as reefs, mangroves and seagrasses, to buffer seawater pH (e.g. Unsworth *et al*., 2012), cope with sea-level rise (Saunders *et al*., 2014), mitigate physical disturbance (e.g. Mumby & Hastings, 2008) and promote ecological resilience across seascapes (e.g. Olds *et al*., 2012). At a broader scale, conserving connectivity will also enable organisms to access refugia from perturbations operating at local to regional scales (e.g. mining; Schlacher *et al*., 2014) to global phenomena (e.g. rising temperatures; Magris *et al*., 2014). Connectivity may also increase the value of ecosystem services provided by seascapes. For example, the value of a coral reef that is well connected to mangroves may be very different from that of a reef which is isolated from complementary resources (Hyndes *et al*., 2014).

FUTURE DIRECTIONS

To date, all studies that have examined whether connectivity benefits conservation have been conducted in reef seascapes (eight on coral reefs; two on rocky reefs) (Appendix S2). It remains to be seen whether similar effects can also be demonstrated in a wider range of seascapes (e.g. coastal wetlands, soft sediments) and at the terrestrial–marine interface (i.e. beaches and estuaries) (e.g. Langlois *et al*., 2005) (priority question 3, Table 1). Research has also largely focused on fishes and should now be expanded to evaluate the conservation benefits of connectivity for other organisms, such as crustaceans (e.g. MacArthur *et al*., 2011) (priority question 4, Table 1).

Of the studies reviewed here, few had attempted to address questions about possible joint functional effects of seascape connectivity and marine reserves on ecological processes (e.g. herbivory, predation, recruitment). Consequently, we do not know whether effects of connectivity on ecological functions are common in reserve networks (e.g. Valentine *et al*., 2008) (priority question 5, Table 1). This is a promising avenue for future research because the influence of connectivity on ecological processes provides the basis for conservation to influence ecosystem resistance and recovery (e.g. Olds *et al*., 2012) (priority question 6, Table 1).

Studying the effect of seascape connectivity on animal movement will shed light on the mechanisms that underpin such spatial ecological relationships, and is key to appreciating how seascape conservation influences dispersal (e.g. Harrison *et al*., 2012). At present, little is known about how the characteristics of seascapes at reserve boundaries (i.e. whether habitat is continuous or patchy) influence movement and dispersal from reserves (Freeman *et al*., 2009; Pillans *et al*., 2014; Pittman *et al*., 2014). Spillover, which is a fisheries objective for many reserves (Halpern *et al*., 2009), will likely be enhanced where habitat is continuous at reserve boundaries, but this will also work against the accumulation of fish biomass in reserves, which is a key conservation objective (Babcock *et al*., 2012; Edgar *et al*., 2014). Studies are needed to measure how the characteristics of seascapes at reserve boundaries influence the frequency and magnitude of spillover from reserves (e.g. Freeman *et al*., 2009; Pittman *et al*., 2014) (priority question 7, Table 1). This will enhance our understanding of the capacity of reserves to achieve a common fisheries objective and thereby improve planning decisions about optimizing reserve design and placement. Given that reserves affect the behaviour and movement of exploited species (Halpern *et al*., 2009; Babcock *et al*., 2010), it will be important to examine whether effects of seascape connectivity on movement, dispersal and habitat use differ between seascapes within reserves, those that span reserve boundaries or areas that are open to fishing.

CONCLUSIONS

We find that the disciplines of landscape ecology and conservation biology lack close integration in the ocean, resulting in few studies that explicitly test for the effects of seascape connectivity on marine reserve performance. By contrast, landscape ecology has proven instrumental in terrestrial conservation (Rudnick *et al*., 2012; Kool *et al*., 2013), and we contend that it will offer similar benefits in the sea. Despite connectivity being increasingly viewed as important in marine conservation, this has generally not translated into quantitative objectives for conservation planning (Magris *et al*., 2014). While this review focused on the implications of seascape connectivity for marine conservation, our findings may have broader implications for spatial conservation planning and ecosystem-based management because connectivity is rarely evaluated when assessing the effectiveness of management initiatives in either aquatic or terrestrial ecosystems. To better integrate connectivity into conservation we must focus research on identifying the mechanisms that underpin connectivity and the functions it delivers for ecosystems. Progress in spatial conservation planning will then be made by linking empirical studies of this nature with theoretical advances in our understanding of connectivity and the scale over which it impacts conservation outcomes.

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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 Summary of seascape connectivity studies in reef and wetland systems.

Appendix S2 Summary of seascape connectivity studies that also quantified marine reserve effects, or were conducted inside marine reserves.

BIOSKETCH

Andrew Olds is a researcher at the University of the Sunshine Coast (Queensland, Australia). His research focuses on spatial ecology, conservation biology and the impacts of global change on marine ecosystems.

The research team includes ecologists from universities and research organizations in Australia, the United Kingdom, the United States of America and New Caledonia who are examining effects of seascape connectivity and marine reserves on faunal assemblages, ecological processes and ecosystem functioning. A.O., K.P. and R.C. conceived and designed the study. All authors contributed to synthesizing published data, analyses, interpreting the results and writing and revising the manuscript.

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APPENDIX: DATA SOURCES USED IN THIS STUDY

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