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Connecting MPAs – eight challenges for science and management

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ABSTRACT

1. Connectivity is a crucial process underpinning the persistence, recovery, and productivity of marine ecosystems. The Convention on Biological Diversity, through the Aichi Target 11, has set the ambitious objective of implementing a 'well connected system of protected areas' by 2020.

2. This paper identifies eight challenges toward the integration of connectivity into MPA network management and planning. A summary table lists the main recommendations in terms of method, tool, advice, or action to address each of these challenges. Authors belong to a science–management continuum including researchers, international NGO officers, and national MPA agency members.

3. Three knowledge challenges are addressed: selecting and integrating connectivity measurement metrics; assessing the accuracy and uncertainty of connectivity measurements; and communicating and visualizing connectivity measurements.

4. Three management challenges are described: integrating connectivity into the planning and management of MPA networks; setting quantitative connectivity targets; and implementing connectivity-based management across scales and marine jurisdictions.

5. Finally, two paths toward a better integration of connectivity science with MPA management are proposed: setting management-driven priorities for connectivity research, bridging connectivity science, and MPA network management.

6. There is no single method to integrate connectivity into marine spatial planning. Rather, an array of methods can be assembled according to the MPA network objectives, budget, available skills, data, and timeframe.

7. Overall, setting up 'boundary organizations' should be promoted to organize complex cross-disciplinary, cross-sectoral and cross-jurisdiction interactions that are needed between scientists, managers, stakeholders and decision-makers to make informed decision regarding connectivity-based MPA planning and management.

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INTRODUCTION

Connectivity is a crucial process underpinning the persistence, resilience, and productivity of marine ecosystems, including exploited marine species (Kritzer and Sale, 2004; Cowen *et al*., 2006; Kool *et al*., 2012; Treml *et al*., 2012) (Figure 1). Overall, connectivity is a primary driver of marine population dynamics (Le Corre *et al*., 2012) at a local and global scale.

Connectivity studies commonly focus on specific habitats, fauna (e.g. fish, turtles, cetaceans, and birds at different stages of their life cycle) (Jacobson and Peres-Neto, 2010), flora (e.g. propagules of mangroves, seagrasses, algae), or floating objects such as plastics, oil, and driftwood (Treml *et al*., 2012) at various spatial and temporal scales (Le Corre *et al*., 2012).

There has been a recent dramatic increase in research effort and a growing diversity of approaches to the study of fish retention and dispersal among populations (see the review of Jones *et al*., 2009). Many of these studies have attempted to capture the spatial dynamics of marine populations, especially with respect to propagule dispersal (Willis *et al*., 2003; Sale *et al*., 2005; Cowen *et al*., 2007).

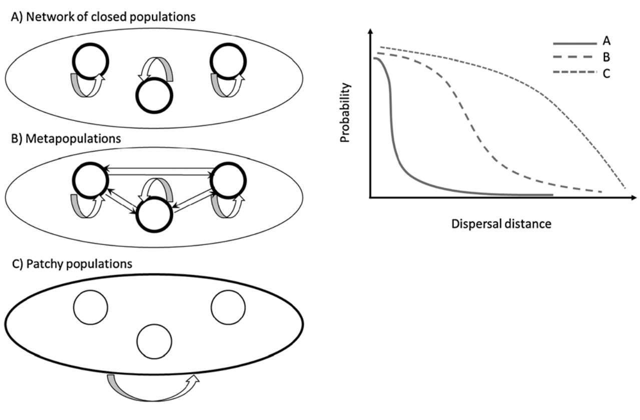

Figure 1. Three spatial models of intra-specific population structure and their associated distribution probability of successful dispersal distance. Small circles are discrete (sub)populations or patches belonging to a regional system are represented by the oval, with dispersal schematized by arrows. Thick lines define the spatial scale of correlation of demographic fluctuations among (sub)populations. Adapted from Kritzer and Sale (2004).

Understanding and quantifying connectivity between habitat patches or spatially disjointed populations is key to support the sustainable management of ecosystems by providing the base data needed for informed decision-making. This understanding is required to prioritize the allocation of conservation effort in the seascape towards, for instance, areas acting as central connection nodes in a network of protected areas. So far, marine protected areas (MPA) networks have mainly been set up with few considerations to connectivity (Magris *et al*., 2014).

Several definitions of the broader concept of 'connectivity' can be found in the abundant connectivity-related literature (Cowen *et al*., 2007; Sale and Kritzer, 2008; Cowen and Sponaugle, 2009; Kadoya, 2009). The widely accepted definition of connectivity is the 'degree to which the (sea)scape facilitates or impedes movement among resource patches' (Taylor *et al*., 1993, 2006). In this paper, connectivity is considered primarily as the flux of individuals among geographically separated subpopulations, occupying discrete patches, in a metapopulation (Cowen and Sponaugle, 2009; Le Corre *et al*., 2012).

Seascape connectivity includes both structural connectivity, i.e. the physical relationships between habitat patches (which is dynamic and influenced by currents, water stratification, etc.), and functional connectivity, i.e. an organism's biological and behavioural response to the seascape structure and dynamics (Kool *et al*., 2012; Baguette *et al*., 2013; Gerber *et al*., 2014).

Understanding connectivity between distant populations is key to their effective conservation and management (Treml *et al*., 2008). Theoretical studies suggest that population connectivity plays a fundamental role in local and metapopulation dynamics, community dynamics and structure, genetic diversity, and the resilience of populations to human exploitation (Hastings and Harrison, 1994; Botsford *et al*., 2001).

Hogan *et al*. (2012) suggest that the persistence and resilience of marine populations in the face of disturbances is directly affected by connectivity among populations. Thus, understanding the magnitude and pattern of connections among populations and the temporal variation in these patterns is critical for the effective management and conservation of marine species.

Connectivity is now widely recognized to be a crucial variable for the design and management of MPA networks through the effects that movements of individuals and genes have on population viability, metapopulation persistence, and resilience to disturbance (Almany *et al*., 2009; Jones *et al*., 2009; Beger *et al*., 2014). A 'well-connected' MPA network is assumed to ensure positive spillover effect by seeding non-protected areas (Halpern and Warner, 2003; Botsford *et al*., 2009; Gaines *et al*., 2010).

In spite of the recent interest and extensive research on connectivity, the effectiveness of the fit of MPA networks with connectivity patterns has unfortunately received relatively little attention. Indeed, MPA set up remains guided by representation criteria rather than persistence criteria, i.e. criteria related to the ecological processes that play an essential role in maintaining ecosystem integrity across time and space (Kritzer and Sale, 2004; Sundblad *et al*., 2011).

As scientific investigation continues, countries are facing increasing pressure to achieve the Aichi Target 11 at regional and national levels. The overall Aichi target is to protect, by 2020, at least 10% of marine and coastal habitats (COP10; www.cbd.int/cop10). The 'Aichi Target 11' specifically mentions that those zonal targets should be achieved through a 'well-connected system of (marine) protected areas'. Since the current fraction of the ocean covered by MPAs continues to grow at a relatively slow rate (Spalding *et al*., 2008; Marinesque *et al*., 2012), the need to expand existing protected area networks has stimulated vigorous debates about their future design (location, size, spatial organization, and flexible zoning) (Rodrigues *et al*., 2004; Moffitt *et al*., 2011; Gerber *et al*., 2014). In addition, the adverb 'well-connected' implies a sufficient knowledge of connectivity patterns and thresholds.

This paper aims to identify and illustrate the major challenges posed by the integration of connectivity into MPA networks management and design. The first section addresses challenges relative to marine connectivity sciences (i.e. knowledge challenges), the second section aims to identify challenges posed by the integration of connectivity targets into MPA networks (i.e. management challenges), and the third section proposes a road map towards better integration of connectivity science within MPA network design and management.

Challenge 1: Selecting and integrating connectivity measurement metrics

There are many methods to estimate marine connectivity already reviewed elsewhere (Jacobson and Peres-Neto, 2010; Le Corre *et al*., 2012): direct observation, mark–recapture techniques, acoustic telemetry, analysis of geochemical and genetic markers, and biophysical modelling. These methods have different strengths and weaknesses, and are applicable to different spatial and temporal scales, and to different species and/or life stages. Since no consensus has yet emerged on a consistent universal connectivity metric, each method relies on a specific definition of the concept of connectivity (Calabrese and Fagan, 2004; Galpern *et al*., 2011). In this section, differences of connectivity estimation methods and the resulting challenges of comparing and integrating their estimates are briefly described. A solution is then proposed through an appropriate study system involving a multidisciplinary approach to help practitioners make more informed decisions regarding the measurement of connectivity.

Connectivity measurement methods differ in their applicability to species (e.g. fish, turtle, cetacean, etc.) and life-cycle stage. The connectivity of juvenile and adult fish can be estimated by the analysis of chemical and genetic markers, mark–recapture methods, acoustic telemetry, and satellite telemetry (Lowe *et al*., 2003; Meyer *et al*., 2010; Grüss *et al*., 2011). Larval connectivity cannot be studied using satellite telemetry or direct marking, but it can be studied using genetic parentage analysis (Christie *et al*., 2010), genetic assignment tests (Saenz-Agudelo *et al*., 2009), biophysical modelling (Werner *et al*., 2007), artificial marking of eggs (Jones *et al*., 2005; Almany *et al*., 2007), trans-generational marking of adult females (Thorrold *et al*., 2006) and direct observation (Shanks *et al*., 2003). Genetic methods have been widely used to infer larval (Christie *et al*.,

2010) and juvenile (Gaggiotti *et al*., 2002) connectivity. Assignment tests are effective when the source populations are well-differentiated, and their precision increases with the number of molecular markers available and their polymorphism (Manel *et al*., 2005). When the source populations are too similar, then assignment tests cannot work. Parentage analysis requires extensive sampling of all potentially connected populations over different cohorts, including both adults and offspring, but yields accurate estimates of connectivity patterns (Christie *et al*., 2010). The main limitation of parentage analysis is the cost and time of sampling. Parentage analysis often provides knowledge on one single-generation because sampling is done on a single cohort of offspring. Thus, the estimation of connectivity's variability requires multi-year studies (i.e. several reproductive seasons). Geochemical methods suffer from similar limitations as assignment tests. If the source population carries too similar of a chemical signature, then it is impossible to assign offspring to a natal location.

The spatial and temporal scale of applicability is a second difference among estimation methods. Biophysical models can provide connectivity estimates over potentially large spatial scales, such as entire sea basins or oceans (Cowen *et al*., 2006; Treml and Halpin, 2012; Andrello *et al*., 2013) and can be used to derive estimates of connectivity over different years, generations, and even projections for the future (Andrello *et al*., in press, a). Conversely, genetic parentage analysis, geochemical markers, egg marking, and trans-generational marking provide estimates of connectivity for only one generation. Given the intense sampling effort required by these techniques, their applicability is also restricted to fine spatial scales. Genetic assignment methods are in-between, because they reveal patterns of connectivity acting over several generations. It seems, therefore, that the connectivity estimates obtained through biophysical modelling can be compared with those obtained through other methods, but only at fine spatial and temporal scales. However, one additional complicating factor is that biophysical models provide estimates of potential connectivity, because they cannot take into account post-settlement processes, while other methods provide estimates of realized connectivity. Comparing estimates can therefore be difficult because post-settlement processes such as mortality and juvenile movements can alter connectivity patterns resulting from the larval dispersal phase (Di Franco *et al*., 2012). In addition, unbiased estimates of connectivity through biophysical models are only possible if sufficient knowledge on larval biology is available to parameterize the models, and if there is an adequately precise hydrodynamic model for the study region. While there is a significant body of literature on the investigation of source–sink dynamics (Sale *et al*., 2005; Roff and Zacharias, 2011), very little is known about the full extent of their life cycles for the vast majority of marine species.

Another scientific challenge is to develop a statistical framework to integrate connectivity estimates derived through different methods. For example, the estimates of potential connectivity derived from biophysical models can inform on the range of possible values for realized connectivity. Various connectivity estimates could be integrated within a Bayesian framework using a clustering method. For example, the range of connectivity estimates obtained using a biophysical model could be used to construct an a priori distribution for estimating connectivity through geochemical or genetic analysis. The high-dimensionality of connectivity measurements can also be reduced using principal components analysis.

Challenge 2: Assessing the accuracy and uncertainty of connectivity measurements

Connectivity measurements are estimated values and are associated with a degree of uncertainty. Uncertainty is the range of connectivity values within which the true value of connectivity is asserted to exist with some level of confidence. Accuracy is the closeness of agreement between measured connectivity and its true value (i.e. the value accepted as true). Biophysical models of larval dispersal can provide estimates of connectivity on virtually any spatial and temporal scale. Knowledge about key biological processes such as larval behaviour, larval mortality, and larval growth is required to derive accurate connectivity measurements (Leis, 2007; Treml *et al*., 2012). Even if all the processes known to affect connectivity measurements in biophysical models can in theory be modelled and integrated, the real limitation to producing accurate model-based connectivity assessments is the scarcity of knowledge and data about larval biology for most species, especially in natural (non-laboratory) conditions. In particular, larval mortality is an extremely difficult parameter to estimate but known to greatly affect the accuracy of dispersal models (Cowen *et al*., 2006). Hydrodynamic models that use coarse spatial resolution or longer time iterations, provide less accurate estimates of current velocities, which results in less accurate overall connectivity estimates (Gaines *et al*., 2003; Largier, 2003).

Recognizing these weaknesses and complementarity of methods, the extent of uncertainties, and the factors affecting the accuracy of modelled connectivity (i.e. trueness and precision) is important to acknowledge. This is particularly important if the connectivity research is designed to be communicated to managers and if the estimates are used to inform the design of future MPA networks. Hogan *et al*. (2012) demonstrate the unpredictable nature of connectivity and highlight the need for more, temporally replicated, empirical measures of connectivity, especially when using this information explicitly to inform management decisions. Indeed, if temporal variability in the pattern and extent of connectivity occurs among populations, connectivity data from multi-year studies would be necessary for confidence in any source–sink patterns. Additionally, researchers should develop further methods and tools to communicate around the uncertainty inherent in their results.

Comparing connectivity measurements using different methods requires matching scientific expertise on their application to different spatial and temporal scales and different species and life stages. A solution to this challenge is to delineate a test area where multiple estimation methods can be simultaneously applied by a multidisciplinary scientific team. The test area should be small enough to apply genetic parentage analysis and geochemical methods. There should be sufficient expertise on larval biology to parameterize the biophysical models. The COMPO project (http://www.compo.ird.fr) is one of the first attempts to bridge the gap between various estimation methods. The project focuses on two species with limited or no adult movement (the damselfish, *Dascyllus aruanus*, and the giant clam, *Tridacna maxima*), and connectivity measurements are derived through biophysical modelling, genetic parentage analysis, and geochemical marker analysis. Crochelet *et al*. (2013) tested a dispersal simulation model against *in situ* observations of young post-larval fish (otolith-derived ages) to investigate a potential connection between two islands in the Indian Ocean. This multi-measurement assessment proved useful for future model-based connectivity assessments in data-poor regions (Ban *et al*., 2009). Comparing independently measured connectivity estimates under similar conditions contributes to evaluating the accuracy of model-based (low cost per km^2) versus field-based (high cost per km^2) connectivity assessments. This comparison is a basis for balancing the cost of each measurement method vs. the benefits for MPA network management.

Challenge 3: Communicating and visualizing connectivity measurements

Using proper terminology to communicate about connectivity measures (e.g. accuracy, uncertainty, trueness, precision, etc.) is needed to facilitate proper communication of results from scientists to decision-makers, the media, and the general public. Communicating connectivity measures to MPA managers, decision-makers, and the global public can be a complicated and complex task. Visual representations of connectivity results include connectivity matrices (Ban *et al*., 2012), network maps displaying nodes linked by lines (Treml *et al*., 2008; Schill *et al*., 2012), polylines or points representing tracking data, streamlines representing simulated flows (Rossi *et al*., 2014), and temporal maps of larvae densities (Crochelet *et al*., 2013). New visualization tools include on-line dynamic maps (e.g. daily turtle tracking data http://seaturtle.org) and simulation models (e.g. CONNIE model http://www.csiro.au/connie2/) accessible throughout computer and smartphone applications (e.g. WhaleAlert downloadable http://stellwagen.noaa.gov/protect/whalealert.html).

When informing on marine spatial management decisions, it is also important that the implications of uncertainties associated with connectivity measurements are communicated. The social implication of results (and their uncertainty) shouldn't be underestimated. For instance, local fisher communities might be strongly affected in their daily life by conservation decisions based on connectivity measurements. Explaining the uncertainty and incompleteness of the best available connectivity measures should be supported by effective communications. Brodlie *et al.* (2012) propose a complete review of the visualization methods of uncertainty associated with those measurements. Morgan *et al.* (2009) synthesized lessons learned by the climate change scientific community to improve communication regarding uncertainty and include: (a) understanding the audience and the information they need regarding connectivity; (b) avoiding complex or obscure language; (c) making connectivity measurements locally relevant through case studies; (d) exploring connectivity visualizations to provide a range of communication opportunities for audiences; and (e) remembering that the provision of connectivity data alone will not stimulate action.

Challenge 4: Integrating connectivity into the planning and management of MPA networks

Maintaining connectivity is widely recognized as an essential objective of marine spatial planning and recent advances regarding ecosystem connectivity necessitate increased integration for marine reserve design (Green *et al.*, 2014). The integration of connectivity into marine spatial planning is the subject of active scientific research, yet applications are rare. In a review of 115 marine spatial applications, Magris *et al.* (2014) found that most of the applications had not effectively incorporated biological processes such as ecological connectivity. Connectivity knowledge should be used not only for the placement of new MPAs, but also for evaluating existing networks and subsequent adaptive management. Existing MPAs identified as key connectivity nodes (i.e. for a population of a given species for instance) should inherit a higher level of importance or responsibility, becoming priority sites for connectivity-oriented management. This 'connectivity-oriented management' should focus on the maintenance of healthy and dynamic populations to preserve and increase exchanges within the network.

Given the complexity, time, and cost of acquiring data for measuring connectivity, the integration of ecological connectivity into the design of MPA networks is often made using surrogate measures of connectivity such as size, shape, and spatial organization of MPAs (Rouget *et al.*, 2003; Almany *et al.*, 2009). Identifying 'connectivity surrogates' can help MPA network design while data collection on connectivity is ongoing (Bode *et al.*, 2012). However, while connectivity surrogates may be a first solution to the problem, they do not explicitly take into account the effects of connectivity on biological processes and the link between biological processes and targets of spatial planning (see Challenge 5 on connectivity targets).

Graph theory has become a popular tool for modelling the functional connectivity of landscape patches (Galpern *et al.*, 2011). This approach informs the ability of a system to offer alternative pathways that can improve overall resilience of a network in the face of environmental changes (Albert *et al.*, 2000; Melián and Bascompte, 2002). Indeed, metapopulations or large systems of sub-populations can be conceived as networks in which nodes are demes (sub-populations), and the links among them symbolize the migration paths (Fortuna *et al.*, 2008; Rozenfeld *et al.*, 2008). Connectivity is thus a prime component of short- and long-term demographic trajectories of metapopulations systems (Hanski and Thomas, 1994; Cerdeira *et al.*, 2005).

Under the conceptual framework of graph theory, candidate sites can be ranked according to their connectivity within a network of sites using various metrics such as 'degree centrality' or 'betweenness centrality' (Calabrese and Fagan, 2004; Rothley and Rae, 2005; Fuller and Sarkar, 2006; Minor and Urban, 2008). Watson *et al.* (2011) used realistic estimates of larval dispersal generated from ocean circulation simulations and spatially explicit metapopulation models to perform such calculations. However, these approaches can be limited if they consider connectivity as a stand-alone entity without accounting for the consequences of connectivity for population persistence (Moilanen, 2011), commonly used in conservation planning. There have been a few attempts to link connectivity to population dynamics in a spatial planning optimization framework through the effects of connectivity on population persistence. These approaches are promising because they permit consideration of connectivity not as a feature per se, but rather through its effects on population dynamics and thus on population persistence. Several studies have improved (marine) protected areas selection algorithms to include objectives of population persistence in single-species (Moilanen and Cabeza, 2002) or multi-species (Nicholson *et al.*, 2006) formulations using a variety of viability metrics (Nicholson and Ovaskainen, 2009), including the probability of population persistence (Moilanen and Cabeza, 2002), the mean time to extinction (Kininmonth *et al.*, 2011), the number of occupied habitat patches (Ovaskainen, 2002), or the metapopulation capacity (Hanski and Ovaskainen, 2000; Nilsson Jacobi and Jonsson, 2011; Andrello *et al.*, in press, b), which all depend on connectivity. The sites selection algorithm optimizes at least one of these metrics to make the persistence target become an operational part of conservation planning (Moilanen and Cabeza, 2002; Nicholson *et al.*, 2006). These methods can be applied to real systems but are not in the form of user-friendly software tools. Marxan (Ball *et al.*, 2009) and Zonation (Moilanen and Kujala, 2008), the most frequently used conservation software for MPA network design, can be used to explicitly consider connectivity as a criterion to optimize the selection of candidate sites for protection. However, they do not consider specific targets of population persistence and the influence of connectivity on population dynamics to drive the selection algorithm. Rather, they use habitat continuity as a measure of landscape connectivity (Ball *et al.*, 2009; Lehtomäki and Moilanen, 2013) and implicitly assume that connectivity is a function of geographic distance. No user-friendly software integrates connectivity as a dynamic and iterative process. The challenge can be met by integrating the persistence-oriented algorithms for protected area selection into tools such as Marxan and Zonation. This requires not only modifying the software, but also an effort of conceptual synthesis between persistence-oriented criteria and representation based criteria. A multi-objective optimization framework (e.g. Marxan with Zones) should be used as a starting point to construct a wider framework where connectivity and population persistence are considered simultaneously with other criteria to drive the protected area selection process. Population persistence criteria should be targeted rather than connectivity per se.

The inclusion of persistence-oriented criteria into multi-objective and multi-species spatial planning tools is only a first step into the consideration of connectivity in marine spatial planning. Indeed, there are many biological processes that are affected by seascape connectivity. As discussed, population dynamics has received considerable attention in spatial planning, but other processes, such as adaptation to environmental change and gene flow, should be included in conservation planning and associated with connectivity. For example, the spread of heat-resistant genes from resistant populations to vulnerable ones can help the latter ones adapt to warming water conditions expected under climate change. It is recommended that this process be taken into account when planning for the location of future MPAs (Mumby *et al.*, 2011). Connectivity also influences gene flow and the maintenance of genetic diversity, which is related to the potential of a species being able to adapt to novel environmental conditions. Indeed, genetic diversity is sometimes considered as a specific target of conservation planning (Vandergast *et al.*, 2008), but the link among connectivity, gene flow, genetic diversity, and spatial planning has yet to be developed. Lastly, the effect of connectivity between protected and unprotected areas has not received enough attention in site selection algorithms, despite the fundamental importance of MPAs as a source of propagules for fisheries.

Thus, the challenge of integrating connectivity into MPA network design can be addressed by (1) developing conceptual links between connectivity (i.e. a feature of the seascape), biological processes (i.e. population dynamics, gene flow, adaptation, larval supply to fished areas), and specific targets for spatial planning (such as ensuring population persistence, maintaining genetic diversity and adaptive potential, increasing fishery yield); and (2) developing site selection algorithms based on specific targets and integration within a comprehensive multi-objective and multi-species framework for spatial planning.

Challenge 5: Setting quantitative connectivity targets

Despite advances in conservation planning protocols during the last two decades, no clear explicit method exists for assigning quantitative objectives (i.e. targets) to ecological processes and therefore a critical need remains to better understand approaches to setting objectives for connectivity (Rouget *et al*., 2003; Magris *et al*., 2014). Quantitative objectives in conservation are essential to support informed, accountable and defensible decision-making regarding marine spatial planning (Game *et al*., 2013).

Connectivity targets are generally set ad hoc, without rationale (e.g. 'rule of thumb') (Magris *et al*., 2014). They are rarely based on quantitative ecological justifications (Watson *et al*., 2011; Bode *et al*., 2012). Quantitative targets, however, can be set for spatial connectivity surrogates (Bode *et al*., 2012) in terms of area and number of replicates. For example, a surface target can be calculated for major connectivity pathways, source or destination patches, or as a percentage of their total area (Rouget *et al*., 2003). Connectivity targets can also be set through connectivity-related parameters such as the minimum size of MPAs, the minimum number of MPAs, and the spacing, grouping and alignment of MPAs (Magris *et al*., 2014). Quantitative connectivity targets can also be expressed for demographic and genetic connectivity. Although demographic and genetic connectivity are both often implicitly assumed when dealing with MPA connectivity, it is important to underline clear differences between both concepts (Lowe and Allendorf, 2010). Demographic connectivity reflects the level of migration needed to significantly influence the demography of receiving subpopulations, without accounting for the fact those migrants may, or may not, reproduce and contribute to the gene pool of the next generation. Quantitative demographic connectivity targets can be set to the 'migration rate,' for instance, as a minimum percentage of incoming migrants that subpopulations may rely on. Genetic connectivity, in turn, does not necessarily require the rate of migrants to significantly affect the demography of the receiving subpopulations, but can be ensured only if a minimum number of migrants effectively reproduce with the receiving subpopulation. Genetic connectivity, therefore, reflects the 'effective migration' or the number of migrants that will effectively contribute to the exchange of genes among subpopulations. Thus, genetic connectivity can be maintained through a very modest amount of migration (e.g. a low quantitative genetic connectivity target), not necessarily sufficient to ensure a significant demographic input to receiving subpopulations. Demographic connectivity targets will equal genetic connectivity targets only in cases where immigrants reproduce and transmit their genes. Consequently, it is important to acknowledge that the coherence of an MPA network should be inferred by ensuring both levels of connectivity are maintained through adequate demographic and connectivity targets, a task that often requires distinct approaches and evaluation processes. It is thus a multispecies, complex problem in need of robust biological data representative of the communities targeted and modelling of a broad range of dispersal scenarios. For example, Coleman *et al*. (2011) showed great differences in the pattern of genetic connectivity for three species of habitat-forming macroalgae along the east coast of Australia, with subtidal species showing higher levels of connectivity across larger distances than intertidal ones.

Challenge 6: Implementing connectivity-based management across scales and marine jurisdictions

Marine spatial planning often mismatches the multi-scalar nature of ecological patterns and processes (Mills *et al*., 2010). The need to address multiple scales in marine spatial planning is widely acknowledged but rarely implemented in practice (Agardy *et al*., 2011). MPA networks are generally designed at a single scalar level (i.e. regional, national or provincial scale), whereas a nested approach at a different spatial scale is recommended to examine the interactions of phenomena, either social or ecological, across multiple scales (Cash *et al*., 2006; Gilliland and Laffoley, 2008). Agardy *et al*. (2011) and Mills *et al*. (2010) suggest integrating marine protected area planning into broader marine spatial planning and ocean zoning efforts. The design of MPA networks is an example of broader scale efforts of marine spatial planning. Nevertheless, the integration of other multi-scale ecological and social processes is still needed to achieve fully integrated and spatially nested ocean zoning (Green *et al*., 2014). Several studies suggest that confronting marine biodiversity erosion, including the disruption of connectivity processes, is going to require regional collaboration and a major scaling-up of management efforts that are focused on increasing knowledge of ecological processes that underlie marine ecosystems resilience (Hogan *et al.*, 2012).

Countries need to work collaboratively to understand patterns in larval dispersal, how distant populations rely on one another, and collaboratively design strategic MPA networks that protect and manage important ecological connections between populations across multiple marine jurisdictions (Treml and Halpin, 2012). The ongoing European-funded PANACHE project between the United Kingdom and France is an illustrative case study of broader ocean zoning efforts across national marine jurisdictions. The aim of PANACHE is to develop a stronger and more coherent approach to the management, monitoring, and involvement of stakeholders for MPAs in the English Channel between England and France. Connectivity has been used as one of the criteria to carry out the assessment of the ecological coherence of the Channel MPA network (Foster *et al.*, 2014). A first approach was to use distance-based thresholds to assess the spacing of MPAs against typical dispersal distances of the features of interest (habitats and species associated with a habitat). The thresholds used come from guidance provided to support the development of the English MPA network (Roberts *et al.*, 2010). This simplified approach is currently followed up by an assessment of the connectivity among the Channel MPA network using a hydrodynamic model for 55 groups of species representing 151 species of interest of the Channel (e.g. species under protection status, species of commercial interest) complemented by enhanced dispersal modelling of the common sole (*Solea solea*), taking into account the life cycle of the species and different egg and larval behaviour. Analyses have shown significant gaps in terms of cross-border connectivity. However, cluster analysis identifies groups of MPAs that could share common management issues. Beyond the results, an increased collaboration between scientific organizations and national MPA agencies of the United Kingdom and France have advanced coordination of scientific research and marine conservation priorities. Indeed, it is critical to collectively set both the connectivity modelling assumptions and the ecological features of interest in order to make the results more useful for MPA planning and establish coordinated management actions across national marine jurisdictions.

Another example of a regional and multi-jurisdictional MPA network planning effort is the Caribbean Challenge Initiative (CCI), launched in 2008 at the CBD Ninth Meeting of the Parties (COP-9). A growing number of Caribbean governments have pledged to expand their MPA systems to include at least 20% of their coastal and nearshore areas by 2020, to develop sustainable financing for these systems, and to adopt adaptive management to ensure long-term viability for marine systems. Figure 2 shows an example of coral reef connectivity simulation that is being used to strengthen regional MPA network planning and design in the framework of the CCI (Schill *et al.*, 2012). Working collaboratively, small island governments have the potential to achieve greater resource leverage and build stronger political will that is more likely to solve complex regional issues such as maintaining connectivity corridors. Large-scale results can be more easily achieved when high level commitments are made under a comprehensive structure for implementation where lessons can be shared and regional capacity increased. By strengthening linkages to global agreements, conservation becomes more relevant to domestic development agendas, which often catalyses the collective commitments of neighbouring leaders.

Challenge 7: Setting management-driven priorities for connectivity research

Recently, there has been a dramatic increase in research efforts and a growing diversity of approaches to better understand marine connectivity, including larval retention and dispersal among populations (see the review of Jones *et al.*, 2009). Many of these studies have attempted to capture the spatial dynamics of marine populations (Willis *et al.*, 2003; Sale *et al.*, 2005; Cowen *et al.*, 2007). However, no framework exists to guide results towards conservation-based or fishery-based priority areas or species.

Setting management-based priorities for connectivity research is required to focus scarce research efforts on issues identified with conservation and fisheries

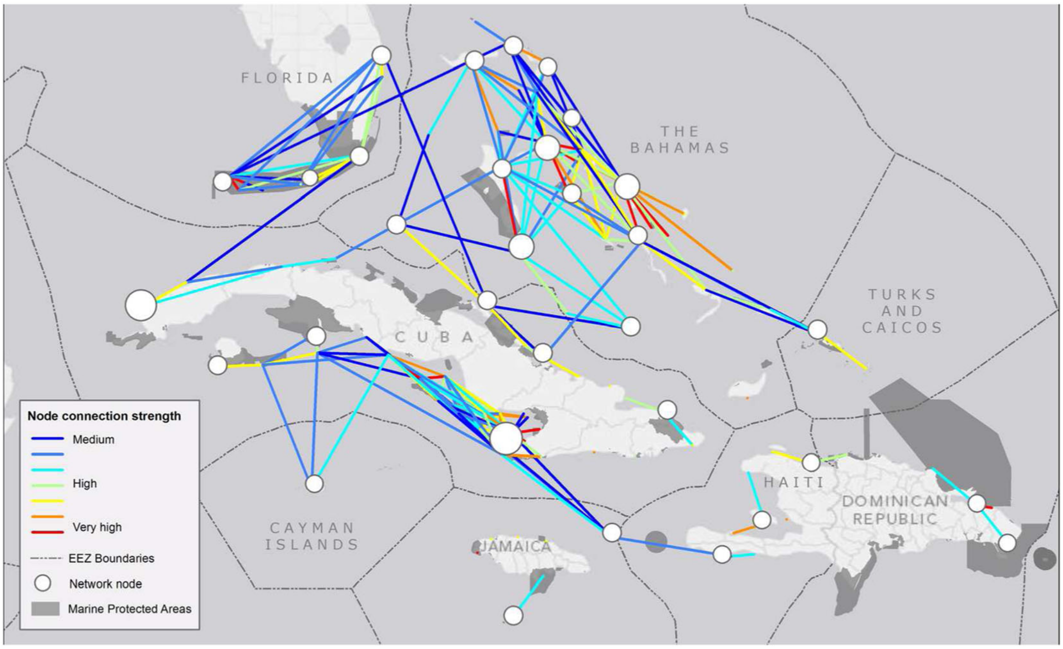

Figure 2. Modelled connections of coral larval retention rates between mapped Caribbean reef units using NOAA's Real Time Ocean Forecast System (RTOFS) data for the years 2008–2011 (Schill *et al*., 2012). Identified nodes indicate important coral larvae source and sink areas that can be used to inform and support regional MPA network planning for the Caribbean Challenge Initiative.

managers. Such priorities can be expressed in terms of species, groups of species, subpopulations, populations, regions, habitat types, habitat patches, connectivity pathways, and other spatial connectivity surrogates. Priorities can also be set in terms of field research (e.g. model-based connectivity assessment, genetics, etc.). From this point of view, management constraints (i.e. limited time and money) are a component of research questions, to identify management-oriented solutions to support connectivity-based MPA network management. However, this is not to say that research should be guided by management, but that research effort in the field of ecological connectivity should be maximized in terms of its potential impact on the way MPA networks are planned and managed. Research priorities should be set through collaboration between scientists and managers (see Challenge 8 for the organization of collaboration).

Thus far, a strong focus has also been made on defining areas that encompass patrimonial or emblematic species, and species targeted as resources or ecosystems considered as vulnerable. Representativity has therefore been a primary focus. Assessing the connectivity of those targeted species and habitats requires a greater research effort (Huston, 1994; Stachowicz, 2001; Bruno *et al*., 2003). It is by no means possible to gain an exhaustive inventory of marine communities associated with a given ecosystem, therefore it is extremely important to be able to define a representative set of species that will, through their importance in maintaining ecosystem functions (e.g. habitat forming, primary producers, etc.) and communities interactions (e.g. apex predators, etc.), be essential for communities, thus contributing to ecosystem persistence. To this purpose, future marine conservation policies should list priority features (e.g. representative species in terms of migratory behaviour) that connectivity research efforts should focus on.

The choice of priority species or habitats for connectivity assessments must take into account priorities identified within international and national policies. International conventions and protocols provide lists of features of conservation importance, such as the Bonn convention for migratory species and the regional seas conventions and protocols (i.e. the Barcelona Convention for the Mediterranean Sea, the OSPAR Convention for the North-east Atlantic, and the Nairobi Convention for the Western Indian Ocean). Similarly, many countries have adapted or developed their own national lists of species and habitats to provide guidance for MPA networks design. From a European waters perspective, the Birds and Habitats Directives have been key drivers toward the development of regional MPA networks, according to the lists of species and habitats referenced in the annexes of those directives. Likewise, the Marine Strategy Framework Directive (MSFD), formally adopted by the European Union in 2008, outlines a legislative framework to reach good ecological status of the European marine water through an ecosystem-based approach to marine spatial planning.

Challenge 8: Bridging connectivity science and MPA network management

Integrating connectivity knowledge into MPA network planning and management continues to be a challenge from both a science and policy perspective (McCook *et al*., 2010). This challenge is echoed in the Aichi Target 19, 'By 2020, knowledge, the science base and technologies relating to biodiversity, its values, functioning, status and trends, and the consequences of its loss, are improved, widely shared and transferred, and applied.' One way to address this challenge is to establish an organization aimed at structuring interactions among a diverse group of actors (i.e. scientists, MPA managers, decision-makers, and multisectoral stakeholders) with the collective goal of integrating connectivity into MPA networks planning. Members of this group already belong to existing organizations such as public institutions, private companies, or NGOs. There is a need to build linkages among such organizations to ensure a continuum from connectivity research to MPA management across scales and marine jurisdictions.

The concept of a 'bridging organization' is particularly relevant to frame interactions among members of single existing organizations. Bridging organizations aim at linking multiple actors from different sectors to solve problems that neither actor would have been able to tackle on their own (Crona and Parker, 2012). The bridging of organizations will expand communication channels

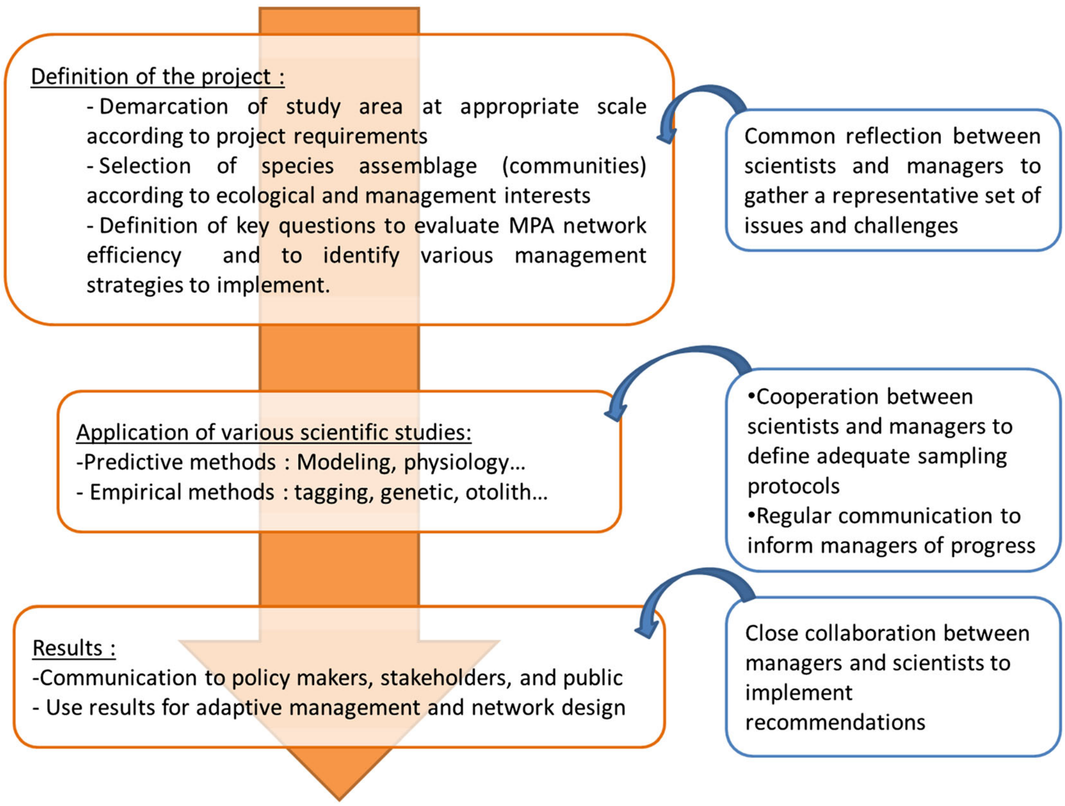

Figure 3. The conceptual framework developed under the MARCO initiative in France to provide a bridge between connectivity science communities and MPA management communities.

Table 1. Summary of findings per challenge

Challenge	Recommendations (method, tool, advice or action)	Scale
1: Selecting and integrating connectivity measurement metrics		
Measuring adults and juveniles connectivity	Chemical and genetic markers	Local
	Mark-recapture methods	Local
	Acoustic telemetry	Local
	Satellite telemetry	Regional
Measuring larval connectivity	Genetic parentage analysis	Local
	Genetic assignment tests	Local
	Artificial marking of eggs	Local
	Transgenerational marking of adult females	Local
	Direct observation	Local
	Biophysical modelling	Regional
Integrating multiple measurements	Bayesian network	Regional
	Principal component analysis	Regional
	Clustering	Regional
2: Assessing the accuracy and uncertainty of connectivity measurements		
Decreasing uncertainty	Increase knowledge on biological processes	Local
	Increase accuracy of hydrodynamic models in biophysical models	Regional
Assessing accuracy and uncertainty	Compare multi-methods estimates in a local test area	Local
	Multi-disciplinary research	Local & Regional
	Balance measurement costs per method vs. benefits for MPA network management	Local & Regional
3: Communicating and visualizing connectivity measurements		
Communicating connectivity measurement	Use a proper terminology	Local & Regional
	Associate connectivity estimates with a level of accuracy and uncertainty	Local & Regional
	Explain uncertainty and its implications	Local & Regional
	Understand the audience and the information they need on connectivity	Local & Regional
	Avoid complex or obscure language	Local & Regional
	Make connectivity measurement locally relevant through case studies	Local & Regional
Visualizing connectivity measurement	Explore connectivity visualizations to provide a range of communication opportunities	Regional
	Connectivity matrix	Regional
	Connectivity maps (network, tracking, densities, etc.)	Regional
	Dynamic map visualization	Regional
	On-line visualization on computer and smartphone	Regional

(*Continues*)

Table 1. (Continued)

Challenge	Recommendations (method, tool, advice or action)	Scale
4: Integrating connectivity into the planning and management of MPA networks		
Integrating connectivity into spatial planning	Develop practical case studies	Regional
	Adjust the size, shape and spatial organization of MPAs	Regional
	Map spatial connectivity surrogates (cheap and rapid)	Regional
Integrating connectivity into spatial planning software	Develop graph-theory-based modelling for site connectivity ranking	Regional
	Integrate connectivity and population persistence criteria into optimization algorithms	Global
	Develop user-friendly spatial planning software that integrates dynamic connectivity	Global
5: Setting quantitative connectivity targets		
Setting feature-based targets	Minimum area and number of patches for major connectivity pathways (and other surrogates)	Regional
	Minimum area and number of patches for source and/or destination patches	Regional
Setting flow-based targets	Minimum migration rate per patch, (sub)population, MPA and/or for the entire MPA network	Regional
Setting MPA-based targets	Minimum area and number of MPAs	Regional
	Spacing, grouping and alignment of MPAs	Regional
6: Implementing connectivity-based management across scales and marine jurisdictions		
Managing connectivity across scales and marine jurisdictions	Implement a spatially nested approach	Local & regional
	Integrate MPA network planning in broader ocean zoning efforts	Local & regional
	Develop cross-country, multi-sectoral cooperations	Local & regional
	Opportunity for governments to achieve broader-scale objectives	Local & regional
7: Setting management-driven priorities for connectivity research		
Setting priorities in terms of biodiversity features	Focus scarce research efforts on priority connectivity issues	Regional
	Set research priorities via a collaboration between scientists and managers	Regional
	Set research priorities for species, regions, and habitats types	Regional
	Identify priority connectivity features for future marine conservation policies	Regional
Setting priorities in terms of research	Set research priorities for connectivity measurement methods	Regional
	Integrate management constraints (cost, time, skills, etc.) into research	Regional
	Promote inter-disciplinary connectivity research	Regional
8 : Bridging connectivity science and MPA network management		
Promoting cooperation between science and management	Organize interactions among scientists, MPA managers, decision makers, and multi-sectoral stakeholders	Local & regional
	Set up “bridging organization”, linking government institutions, NGOs, science groups, and MPA agencies	Local & regional

linking stakeholders, policy makers, and scientists altogether. Brown (1991) argued that the idea of bridging organizations is key to an emerging 'multisectoral' development paradigm. Such interactions are designed to relate different scales of governance and provide arenas for knowledge sharing, collaboration, and learning, and overall adaptive co-management (Leys and Vanclay, 2011). The underlying hypothesis of 'bridging organizations' is that collective learning, through iteration, is superior to fragmented knowledge distributed among single organizations. In the case of marine conservation planning, those organizations are government institutions, NGOs, science groups, and MPA agencies. The Large Marine Ecosystem (LME) organization implements ecosystem-based management and is currently underway in 110 economically developing countries. It is a sound example of a bridging organization between science and management across marine jurisdictions (Sherman, 2014). The Great Barrier Reef (GBR) also provides a globally significant demonstration of the effectiveness of large-scale networks of marine reserves in contributing to integrated, adaptive management by linking up scientists with MPAs managers (McCook *et al*., 2010). In France, the research group on Marine Connectivity (MARCO) is an illustrative example of a bridging organization dedicated to marine connectivity issues. MARCO brings together scientists involved in connectivity assessment in distinct fields (modelling, tagging, tracking, or population genetics) with executive officers of the French MPA agency. The first output of this collaboration is a conceptual framework (Figure 3) that organizes interactions among scientists and MPA agency officers along a conservation planning process: definition of objectives, connectivity assessment (e.g. methods, field data collection, data analysis), and communication of results. This framework aims to improve the design and the management of the French MPA network by easing and framing interactions among scientist and managers.

CONCLUSION

This paper identified eight challenges toward the integration of connectivity into MPA network management and planning. As a summary of findings, Table 1 lists the main recommendations in terms of methods, tools, advice, or actions to address each of those challenges. There is not a single method to integrate connectivity into marine spatial planning. Rather, an array of potential solutions can be assembled according to the MPA network objectives, area, budget, available skills, data, and timeframe. Addressing each challenge is a complex task and requires inter-disciplinarity and cross-sectoral cooperation between scientists, managers, stakeholders, and decision-makers. Setting up boundary organizations will promote this cooperation to make informed decisions regarding connectivity measurement methods, quantitative connectivity targets set up, visualization of connectivity measurements (estimates and uncertainties), and overall, MPA network planning and management.

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