Marine connectivity in spatial conservation planning: analogues from the terrestrial realm

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Abstract

Context Spatial prioritization is an analytical approach that can be used to provide decision support in spatial conservation planning (SCP), and in tasks such as conservation area network design, zoning, planning for impact avoidance or targeting of habitat management or restoration.

Methods Based on literature, we summarize the role of connectivity as one component of relevance in the broad structure of spatial prioritization in both marine and terrestrial realms.

Results Partially diffuse, directed connectivity can be approximated in Zonation-based multi-criteria SCP by applying hydrodynamic modelling, knowledge on

species traits, and information on species occurrences and quality of habitats. Sources and destinations of larvae or propagules can be identified as separate spatial layers and taken into account in full-scale spatial prioritization involving data on biota, as well as economic factors, threats, and administrative constraints. While population connectivity is an important determinant of metapopulation persistence, the importance of marine connectivity depends on species traits and the marine environment studied. At one end of the continuum are species that occupy isolated habitats and have long pelagic larval durations in deeper sea areas with strong directional currents. At the other extreme are species with short pelagic durations that occupy fragmented habitats in shallow topographically complex sea areas with weak and variable currents.

Conclusions We conclude that the same objectives, methods, and analysis structures are applicable to both terrestrial and marine spatial prioritization. Marine spatial conservation planning, marine spatial planning, marine zoning, etc., can be implemented using methods originated in the terrestrial realm of planning.

Keywords Marine connectivity · Ecosystem services · Systematic conservation planning · Marine spatial planning · Zonation software

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Introduction

Connectivity is a fundamental component of spatial ecology and a target of conservation in its own right, as evidenced by the field of connectivity conservation (Hanski and Ovaskainen 2000; Crooks and Sanjayan 2006; Kool et al. 2013). While generally agreed to be of relevance for conservation planning, accounting for population connectivity turns out to be very complicated at the operational level. The spatial scale of connectivity required is different for a home range, local population, regional metapopulation or for connectivity needed to allow range shifts following climate change (Hodgson et al. 2009; Mokany and Ferrier 2011; Gerber et al. 2014; Magris et al. 2014). Connectivity depends on temporal scale and can be different between daily movements, seasonal movements and long-term distribution changes (Kool et al. 2013). Further, connectivity is different depending whether it happens passively or actively, on the ground or through air or water, and whether the organism moves itself or is carried by others, as is the case for many invasive species carried by humans. Physical barriers may influence connectivity strongly, at times totally restricting connectivity between sub-populations. Scaling of connectivity is also highly specific to species-group, ranging from meters for sessile plants, algae, molluscs and certain corals (Shanks et al. 2003), to almost global for whales and some migratory birds.

Additional to ecological considerations, connectivity interacts with the human dimension. Land ownership may impact land use decisions, which needs to be accounted for when integrating connectivity in conservation planning. Pressures (threats) are often linked to the presence of people (destructive human activities), which disrupt connectivity of populations (Joppa et al. 2016). A form of human dimension connectivity is also the demand and equitable availability of ecosystem services, and associated accessibility (Kukkala and Moilanen 2017). The effectiveness of conservation actions may be impacted by the spatial aggregation (connectivity) of protected sites in relation to human pressures (Crooks and Sanjayan 2006; Kool et al. 2013). Overall, it follows that connectivity is conceptually highly relevant for management and planning decisions but dealing with connectivity operationally may appear confusing.

Connectivity has long been studied in the context of habitat fragmentation and, consequently, most

applications of connectivity are from the terrestrial realm. For instance, the ISI Web of Science finds (in May 2019) over 20,000 studies on topic “(species or population) AND connectivity”, but when the qualifier “AND marine” is added to the search phrase, the number of found records declines to 2500. This discrepancy stems from practical obstacles for measuring dispersal rates in the marine environment, and from an earlier paradigm that marine populations are demographically “open” and therefore naturally highly connected. Long pelagic larval durations (PLDs of many weeks to over one year) in many marine species, coupled with predicted advection of passive or semi-passive larvae and propagules by oceanic currents, were taken to imply that long-distance dispersal among subpopulations may be a pervasive phenomenon (Cowen et al. 2000; Becker et al. 2007). A wealth of research has since confirmed this perception to be inaccurate, and that marine connectivity is often strongly modified by both demographic and behavioral traits of species and variation in oceanographic processes (Cowen and Sponaugle 2009; Olds et al. 2018; Balbar and Metaxas 2019, and references therein).

Consequently, connectivity can be a major determinant of marine community structure and ecosystem functioning. Many marine organisms have several life history stages which occupy different habitats, and exchange of individuals between sub-populations is necessary for metapopulation persistence (Cowen et al. 2007; Cowen and Sponaugle 2009; Watson et al. 2012). Marine connectivity studies have therefore investigated dispersal of propagules, such as seeds, spores, eggs, plant fragments, larvae and juveniles (Jones et al. 2009; Harrison et al. 2012; Green et al. 2015; Selkoe et al. 2016; Johannesson et al. 2018), estimated connectivity in a changing environment (Gerber et al. 2014; Magris et al. 2014; Coleman et al. 2017; Jonsson et al. 2018), and the relationship between estuarine and coastal systems and land-sea interface (Vasconcelos et al. 2011; Tétard et al. 2016; Perez-Ruzafa et al. 2019). Especially for fragmented populations the key question is whether the habitat is large enough for the population to be self-seeding, or if propagules from adjacent subpopulations are needed for local population maintenance. This question has been addressed by a large number of studies where the importance of population connectivity on the functionality of marine protected

area networks has been studied (e.g. Palumbi 2003; Christie et al. 2010; Berglund et al. 2012; Soria et al. 2014; Green et al. 2015; Balbar and Metaxas 2019; Ortodossi et al. 2019).

Planning of multiple uses of ocean space conceptually intertwines with similar questions in the terrestrial realm. Which areas can be reserved for conservation and which for, e.g., offshore energy production or marine mineral extraction? Where building of a port or a major bridge jeopardizes marine biodiversity and its ecosystem services? Such questions of marine spatial planning benefit from practical tools and analyses that support decision making. For instance, the Atlantis ecosystem model considers biophysical, economic and social aspects (Link et al. 2010), The Cumulative Impacts Assessment (Menegon et al. 2018) and Cumulative Human Impact (Halpern et al. 2019) tools allow for estimation of multiple pressures to marine ecosystems. The Integrated Valuation of Ecosystem Services and Tradeoffs tool (InVEST) aims to estimate how ecosystem services are influenced by human activities and climate (Nelson et al. 2009), and Marxan (Ball et al. 2009) implements target-based planning, where a representation target level is specified for each species/habitat and an optimal minimum cost solution is then sought.

What then differentiates marine connectivity from its terrestrial counterpart? Many marine species have a larval stage with weak or negligible swimming capabilities, and connectivity in the marine environment is therefore foremost physically driven, dictated by the horizontal and vertical movement of the water (ocean currents, wave action, upwelling, etc.), which may vary inter-annually, seasonally and in short term. Rapidly developing field of research, that aims to resolve how physically driven connectivity should be taken into account in designating marine protected area networks, is the graph theoretic approach and network analysis (Treml et al. 2008; Kininmonth et al. 2011, 2019; Krueck et al. 2017; Treml and Kool 2018; Fox et al. 2019; Friesen et al. 2019), which can be coupled with oceanographic and biophysical modelling that integrates the physics of the ocean and the characteristics of species (Watson et al. 2012; Thomas et al. 2014; Lequeux et al. 2018), including the effects of larval traits and habitat quality (Berglund et al. 2012; Corell et al. 2012; Jonsson et al. 2016; Magris et al. 2016).

There is always a tradeoff between the level of realism and applicability of approaches to spatial conservation planning. In some cases there may be sufficient information for the credible application of some form of direct spatial population dynamical modelling (Burgess et al. 2014; Lett et al. 2015; Treml et al. 2015; Kininmonth et al. 2019). In many cases, data for the reliable parameterization and optimization on top of species-specific meta-population dynamical models are not available, and some simpler approach is called for. Therefore, the present work concerns generic approaches to spatial prioritization based on distribution data, the most common type of data available for spatial planning.

Two major generic approaches to spatial conservation planning are embodied by the software packages Marxan (Ball et al. 2009) and Zonation (Moilanen et al. 2005; Lehtomaki and Moilanen 2013), which are different both conceptually and operationally. At the very highest level of description, these approaches can be characterized as follows. Marxan implements target-based planning, in which the minimum performance characteristics of the solution are specified in advance for all biodiversity features (the targets) and the emergent property of optimization is the budget needed to satisfy targets. Zonation on the other hand implements a set of principles that apply to an arguably well-justified, balanced and cost-efficient priority ranking solution. The balance between species (the coverage of each species) is an emergent outcome of analysis and the budget can be selected post-hoc. Marxan operates on polygons (pre-defined planning units) whereas Zonation operates on high-resolution grids that model, among other things, variable habitat quality and costs. Recently, Marxan Connect implemented a host of graph-theoretic connectivity (Minor and Urban 2007) measures into Marxan analysis (Daigle et al. 2018). There are examples of the use of Marxan and Marxan Connect in the marine context (Beger et al. 2010; Weeks 2017; Daigle et al. 2018), but we will not repeat this previously published material here. Rather, we draw from terrestrial parallels and investigate the role of the connectivity methods of Zonation (version 4) in marine spatial prioritization, which is poorly covered by prior publications. In contrast to the graph-theoretic methods of Marxan, most of these methods are based on kernel-based, declining by distance, connectivity calculations on high-resolution grids.

We start by outlining the role of connectivity in spatial prioritization and the role of marine partially directed diffuse connectivity among other forms of connectivity. We then summarize how forms of connectivity can be incorporated together with other factors such as economics, human pressures and administrative constraints, in Zonation-based multi-criterion MPA network design. An operational solution, drawing on the factors accounted by (Jonsson et al. 2020) in the Baltic Sea, is suggested for the approximation of diffuse marine connectivity. The practical considerations we identify, and the conclusions we make, are broadly relevant for marine spatial planning and marine spatial conservation prioritization in general.

Data requirements for a balanced solution in SCP

Before considering the role of connectivity in SCP, it is useful to consider different data types common in spatial prioritization, which commonly uses hundreds or thousands of spatial layers as inputs. These data broadly represent ecology, economics, threats and administrative restrictions (Fig. 1) (Kujala et al. 2018a):

1. **Ecology.** Primary ecological data describes distributions of species and habitats (ecosystems, biotopes, communities). Closely associated is ecosystem service (ES) provision, which arises from species and habitats, but with ES there are further considerations of supply and demand and of equitable availability (Kukkala and Moilanen 2017). Obviously, species, habitats and ES are all relevant both in the terrestrial and the marine realms.
2. **Economics.** Incorporating economical costs facilitates cost-effective planning and promotes societal acceptability of conservation efforts (Naidoo et al. 2006; Kukkala and Moilanen 2013). Costs can be divided into direct costs of conservation and opportunity costs, which represent lost income by stakeholders due to, e.g., fisheries no-take zones. Again, costs are relevant for both terrestrial and marine applications.
3. **Threats,** a.k.a. pressures, stressors, drivers represent human activities that degrade the environment and which should be counteracted (Joppa et al. 2016). Threats can be stoppable, such as resource extraction, partially stoppable, such as human disturbance, and effectively unstoppable by local action, such as waterborne pollution or climate change. Stoppable threats can be prioritized for action whereas unstoppable threats cannot be addressed through protected area network design. Again, threats are relevant for both realms.
4. **Administrative restrictions,** including land (water) ownership, or areas restricted for specific activities, such as nature conservation, energy production, military activities or aviation, etc. These data typically constrain the spatial pattern that can be prioritized for action. Again, this category of data is relevant for both terrestrial and marine applications, which brings about an interim conclusion that there is nothing fundamentally different between the broad requirements and data demands of SCP in terrestrial and marine realms.

From Fig. 1 it becomes evident that connectivity is an important factor that comes in numerous forms and depends on the amount, quality and spatial distribution of habitat, which are the primary drivers of biodiversity persistence. At the same time connectivity influences other biodiversity features, such as ecosystem services. It is however as evident that connectivity is only one factor influencing spatial prioritization. A host of societal considerations under the categories economics, threats and administrative restrictions also impact the prioritization, and connectivity is also intertwined with societal forms of connectivity, accessibility (connectivity) of ES to people.

Forms of connectivity and implementation options relevant for marine SCP

Connectivity has a fundamental role in both terrestrial and marine spatial ecology, since it links structural aspects of the landscape to the demography and persistence of populations. From the perspective of a species, the two most elemental aspects of landscape (and seascape) structure are habitat area and quality, which determine the carrying capacity of the landscape (Hodgson et al. 2009). Connectivity follows from habitat aggregation (opposite of fragmentation)

Fig. 1 Position of connectivity in spatial prioritization. Ecological connectivity is relevant for species, habitats and ecosystem services. Note that only connectivity has been

expanded out in detail in the diagram: other higher-level factors could be similarly expanded as well

and influences via metapopulation dynamics the fraction of carrying capacity utilized (Hodgson et al. 2009). It is broadly accepted that sparse and fragmented habitat networks may lose connectivity and consequently metapopulation viability (e.g. Hanski and Ovaskainen 2000). Whether a habitat network is occupied by a species is much dependent on the density of habitat across the landscape (e.g. Hanski and Ovaskainen 2000).

Connectivity is usually considered as an ecological process, determined by an interaction between demographic and behavioral parameters of species and their physical environment. For the purposes of a multicriteria analysis supporting SCP, also other forms of connectivity need to be accounted for Table 1 (the three left-hand columns) summarizes forms of marine and terrestrial connectivity relevant either from the ecological or societal perspective.

It is notable that most forms of connectivity are common to both environments, except for the final one, partially directed diffuse connectivity (PDDC). In the terrestrial environment, seeds, spores and other propagules may be carried laterally by winds, but the direction is rarely strongly directed. In the marine environment, in contrast, there are several types of directed processes including oceanic currents, different scale gyres, wind-induced water movement, tides, river discharges, and coastal upwelling, that may transport propagules of marine organisms hundreds of meters vertically and tens or hundreds of kilometers laterally (Shanks et al. 2003; Jones et al. 2009; Harrison et al. 2012). The same processes also facilitate the spread of less welcomed agents, such as contaminants and pathogens (Kough et al. 2014).

In Table 1, we also summarize how the different forms of connectivity can be implemented in SCP (the three right-hand columns). The decision support tool

Table 1 Forms of connectivity and implementation options for marine connectivity in SCP. Options for implementing connectivity during (i) data preprocessing, possibly using external tools, (ii) during Zonation priority ranking analysis, and (iii) after analysis in post-processing either within or outside

Zonation. A question mark = no satisfactory implementation is known to us. Techniques marked L&M13 are summarized and original citations can be found e.g., in Lehtomäki and Moilanen (2013)

Type of connectivity	Terrestrial, marine, or both	Explanation	Implementation in SCP		
<i>Primarily ecological connectivity needs</i>			Pre-processing	During analysis	Post-processing
Structural contiguity	Both	Size of structurally connected patch, associated with home range size, minimum viable population size (habitat area) and local population persistence (e.g. Hanski and Ovaskainen 2000)	Use of large enough selection units	Boundary length penalty. As by-product of functional connectivity methods. (L&M13)	Filtering of too small areas
Functional, scaled (declining) by distance	Both	Declining-by-distance, species-specific scale of landscape use. Also relevant for species with passive dispersal such as wind dispersed seeds or marine species larvae. Can be scaled, e.g., according to home range size, area needed by local population or dispersal capability of species	e.g., smoothing kernels applied on distributions	Distribution Smoothing; Boundary Quality Penalty; Matrix Connectivity (L&M13)	Selection of patch networks that have short enough inter-patch distances
Path-like; corridors	Both	Connectivity guided through very specific habitats, which can be corridor-like remnants of previously more widespread habitats. Dispersal may be blocked by barriers (motorways, artificial structures in seascape, physical barriers (anoxia, thermocline, etc.)). (Tétard et al. 2016; Bishop et al. 2017; Johannesson et al. 2018)	Precomputed connectivity surfaces, Circuitscape, etc. Forcing of known bottlenecks into solution	Corridor-Zonation (Pouzols and Moilanen 2014)	Spatial overlay by corridors developed elsewhere
Strongly directed	Terrestrial (riverine) marine	Water flows downriver; sea areas with strong and consistent marine currents	Precomputed current velocity fields with connectivity patterns	Zonation freshwater connectivity (L&M13)	Inclusion of large river segments, including headwaters, into conservation plan

Table 1 continued

Type of connectivity	Terrestrial, marine, or both	Explanation	Implementation in SCP		
Diffuse 2D, directed by landscape structure and pattern of habitats	Both	Diffuse movements of animals guided by habitat pattern and preference as well as variable movement rates and mortalities of species in different habitats (Ovaskainen et al. 2019)	See next section		
Connectivity interactions	Both	Interaction e.g. between predator and prey, present and future distribution, or (negative interaction) between species and disturbance (threat, pressure) (Rayfield et al. 2009)	GIS overlays or pairwise connectivity transforms	Pairwise connectivity interaction (positive or negative) (L&M13)	?
Network-level connectivity	Both	Maintenance of sufficiently high regional habitat density that viable metapopulations are preserved	Inclusion of data that emphasizes landscape-level key locations for connectivity	Arises from application of functional connectivity in analysis	Delineation of dense enough (however defined) networks of areas
Connectivity in environmental space (as opposed to geographic space)	Both	Based on environmental similarity in addition to geographic proximity. Relevant for long-distance, long-time, distributional changes following, for example, environmental change due to climate warming. May require large corridor-like elements with environmental gradients (Mokany and Ferrier 2011)	?	e.g. specialized quantitative analysis methods (Mokany and Ferrier 2011)	Post-hoc overlay with corridors over suitably chosen environmental gradients
Partially directed, diffuse, possibly 3D	Marine	Partially directed, diffuse, connectivity due to physical drivers, e.g. ocean currents, waves, winds, tides and river discharges. Characteristic to marine environments and most relevant to species with passive dispersal	See next section		

Table 1 continued

Type of connectivity	Terrestrial, marine, or both	Explanation	Implementation in SCP		
<i>Primarily human-motivated connectivity needs</i>					
Logistic	Both	Size and connectivity requirements influence conservation area establishment and management. A few large PAs are less expensive to design and maintain than many small (Ball et al. 2009). Such design also contributes to cost-efficiency and hence social acceptability of conservation (Fernandes et al. 2005)	Use of large enough selection units. Choice of analysis area itself	Additional aggregation via the BLP	Filtering of areas by size and possibly other factors
Accessibility	Both	Accessibility of ES to people, associated with the connectivity between supply and demand	Utilize precomputed relative accessibility surface	e.g., use accessibility surface as feature, or in a connectivity interaction or in condition transform	GIS overlay of priority rank map and accessibility map
Negative (threats)	Both	Spatially correlated degradation of habitat quality due to some pressure such as pollution, hunting, or invasive species	Inclusion of threat layer as negatively weighted feature (for avoidance)	Negative connectivity interaction (L&M13)	GIS overlay with avoidance of areas under threat
Equitable availability (e.g., ES)	Both	Implies dispersed availability of ES (Kukkala and Moilanen 2017; Verhagen et al. 2017)	Separate feature layers for sub-areas (Verhagen et al. 2017)	Analysis with automated administrative units division (Pouzols et al. 2014)	Selection of regional priority areas for biodiversity and ES

specifically referenced here is Zonation, which develops a balanced spatial priority ranking through the full analysis area and is applicable both to conservation planning and ecological impact avoidance. Zonation can balance many biodiversity features, habitat quality, multiple cost components, threats and administrative constraints. Also multiple forms of connectivity, including several declining by distance, kernel-based methods have been available since 2005 (see Lehtomäki and Moilanen 2013 for references). A more thorough review of Zonation is available in a recent marine application based on extensive data in the

Finnish waters (Virtanen et al. 2018), a recent global analysis that includes both terrestrial and marine areas (Di Minin et al. 2019) and in a summary of Zonation methods (Lehtomäki and Moilanen 2013).

The main conclusion from Table 1 is that many terrestrial connectivity methods are transferable to the marine realm and therefore applicable to marine SCP, and practical methods to account for them exist in spatial prioritization tools, such as Zonation. The implementation of the connectivity forms typical for the marine realm, PDDC, in SCP is explained in more detail in the next section.

On the approximation of partially directed diffuse connectivity

A simple qualitative approach to incorporate PDDC in spatial prioritization is to identify and utilize marine habitats (e.g. reefs, inhabited by many sessile macroalgae and invertebrates, or underwater sandbanks, occupied by seagrasses) that are important sources and /or destinations of dispersal propagules (Jonsson et al. 2020). Spatial data on these habitats can then be added into analysis that elevates priorities of these regions in SCP. Expressed in a more recipe-like manner in the context of Zonation:

0. Starting point. Develop spatial prioritization setup that includes all normal components relevant for your application, including some combination of distributions of biodiversity features (species, habitats, ecosystem services), costs, opportunity costs, threats, administrative restrictions, and ecological parameters such as connectivity (Lehtomäki and Moilanen 2013; Kukkala and Moilanen 2017; Kujala et al. 2018a).
1. Add distributions that approximate PDDC (described below), to elevate priorities in areas relevant for it. Remember that PDDC is probably only relevant for a subset of features included in analysis.
2. Run analysis as usual, for a recent application in the marine realm see Virtanen et al. (2018).

Here, the key is the layers (spatial grids) that represent the approximation for PDDC. Develop two or three layers per species, species group, or habitat, as relevant for your application. These layers are:

- (i) The distribution map for the feature, a basic building block of spatial prioritization. This layer typically models local habitat quality on continuous scale, possibly using some statistical distribution modelling technique (for a review see e.g. Norberg et al. 2019). This layer represents where the feature is; you cannot protect species or habitats where they do not occur. Note that for most species effects of habitat quality are much stronger than effects of connectivity and that connectivity derives from habitat quality; there is no connectivity without quality (Hodgson et al. 2009). Persistence of populations is of course

positively correlated with both area and habitat quality.

- (ii) Possibly add separate “source map” that represents the outflow of dispersing larvae or individuals (e.g. Jonsson et al. 2020). At first approximation this could be the same map as the previous one. However, a separate feature layer can be developed to allow distinction between local habitat quality and export of propagules (converse of retention), which depends on the structural complexity of the seascape and hydrodynamic flows in the region. Development of this layer will utilize a biophysical flow model, described below.
- (iii) Add map of local habitat quality (layer i) weighted by inflow of dispersing propagules. These locations are well connected to the network. Also, this layer is developed using the flow model.

To obtain a more quantitative estimate for the effects of biophysically driven connectivity, (i) a hydrodynamic model projecting particle trajectory, (ii) information on larval longevity, and other relevant traits, and (iii) habitat quality maps for the species of interest are needed. Of these, the hydrodynamic information is compulsory. Presence–absence habitat distribution data and a generic decay function can be used if more detailed information on larval traits and habitats is missing. Based on this information, input PDDC layers are produced in the following manner.

Depending on local habitat quality, assign each grid cell a number of dispersing propagules. Use the external flow model to diffusely disperse those propagules across the seascape. Use a decay function to model death of propagules during the process. For each grid cell, keep track of where propagules end up. Also, save the number of propagules arriving to each cell. As a result, two layers are obtained, (i) one for how many propagules the cell contributes to the network (source layer), and (ii) one for how many propagules the cell receives from the network (destination layer). As different species or species groups can have different habitat requirements and dispersal parameters, the process should be replicated as necessary.

When the PDDC layers described above are added into the spatial prioritization setup, priorities become elevated for locations that have (i) high local quality

for features, (ii) high export of propagules that reach other sites, and (iii) high inflow of propagules. The most valuable habitats are locally good quality and both export end receive lots of dispersing propagules. The least valuable habitats are low quality and isolated, with small or missing flow of dispersing propagules. These effects become balanced across all features in analysis. The overall effect of single data layer is expected to be small, because the priority ranking is an balancing over many layers of information with one layer only representing a minor fraction of the totality (Kujala et al. 2018b).

The benefit of this approach is that completely independent simulation models for larval dispersal can be used to develop the input layers, which can then be entered into SCP. While this approach is conceptually simple, we recognize that getting sufficient data about habitat distributions and dispersal parameters may not be easy, and that simulating circulation and larval dispersal at a high resolution over large areas can be computationally demanding.

Zonation-technically, the aggregate weight of the PDDC layers should be set in relation to all other factors included in analysis (see Fig. 1). Using hierarchical division of weights (Lehtomäki and Moilanen 2013), the weight of individual PDDC layers can be further adjusted accounting for the relevance of PDDC for the particular species, species group and/or habitat.

Discussion

Marine and terrestrial organisms obviously differ and have different distribution drivers. Even so, the broad principles that govern protected area network design and spatial conservation prioritization are largely the same (Kukkala and Moilanen 2013; Kujala et al. 2018a). For both, it is desirable to conserve species and habitats; conservation areas should form networks; individual protected areas should be large enough to support viable populations; and threats should be identified and counteracted cost-effectively (Naidoo et al. 2006; Joppa et al. 2016; Kujala et al. 2018a).

There are certain features that are typical for marine connectivity, however. One important distinction is that many marine organisms, both fish and invertebrates, utilize different habitats during different life history stages (Ayre et al. 2009; Cowen and Sponaugle

2009), which needs to be considered when assessing the effects of connectivity for metapopulation persistence. It is also notable that in marine environments direct measurements of dispersal are still rare, and mostly concern larvae of coral reef fish (Almany et al. 2007; Planes et al. 2009; Harrison et al. 2012). In the majority of studies connectivity is inferred with graph-theoretic approaches or using biophysical analyses based on oceanographic models and knowledge on species traits affecting dispersal (Cowen and Sponaugle 2009; Balbar and Metaxas 2019, and references therein).

Here we have concentrated on pointing out the applicability of terrestrial SCP connectivity methods in the marine environment (Fig. 1; Table 1), and specifically when using the Zonation approach to spatial prioritization. The same connectivity techniques can be used for dealing with patch size, functional connectivity, connectivity interactions (positive and negative), accessibility, distributed provision of ES, and network-level structure that arises from these. Mainly only partially directed, diffuse connectivity (PDDC) needs to be accounted for by different techniques than in terrestrial environments.

How relevant is this type of connectivity for SCP in the marine environment? As outlined above, it depends on interaction between the dispersal characteristics of the organism and the physical properties of the marine area of interest. Different patterns are likely to emerge between shallow, topographically complex areas with mosaic habitat patterns, and deeper areas where habitats suitable for target organisms are located further apart. Dubois et al. (2016) and Largier (2003) pointed out that flow speeds are typically slow near the shore, due to the coastal boundary layer, which retains, e.g., fish larvae in the near-shore areas. Nickols et al. (2015) showed that coastal boundary layer decreases dispersal distances by 59%, and increases self-retention of larvae by three orders of magnitude. Almany et al. (2007) and Andutta et al. (2012) concluded that dispersal of coral reef propagules is slowed down by the “sticky water” of dense reef areas, which generates hot spots of self-seeding within the reefs. Similar hydrodynamic phenomena occur also in fragmented archipelagos, with strong seabed shear and variable current patterns, which makes dispersal substantially shorter and more stochastic than in deeper open sea areas.

To sum up, partially directed, diffuse connectivity is most relevant in marine environments where species occupy somewhat isolated habitats and rely on passive drift, and where significant directional currents prevail. In contrast, in sea areas where water movement patterns are fluctuating, weak, stochastic or without much direction, such as in complex reef areas (Andutta et al. 2012) then directional currents will have a relatively smaller effect for metapopulation persistence. This is likely to be the case also in complex archipelagos, such as those in the northern Baltic Sea, where species niches are fragmented (Virtanen et al. 2018), currents variable and depend on short-term variation in wind direction and air pressure (Tuomi et al. 2018). In such areas, other parameters, such as habitat quality and productivity, probably override vague connectivity effects (Fig. 1; Kujala et al. 2018a), and radially symmetric, declining by distance, connectivity responses may be perfectly sufficient approximations for spatial prioritization.

It is also notable that in fragmented shallow water environments, many functionally important species occur both inside and outside the MPAs. They therefore receive propagules not only from neighboring MPAs, but also from other areas occupied by the species. In such cases it is necessary to assess dispersal of propagules not only between MPAs, but also between all habitats where the species may occur. For such species, a full-scale spatial prioritization (Virtanen et al. 2018), or a more comprehensive localization of the subpopulations combined with a posteriori analysis of the MPA network (Jacobi et al. 2012), is necessary to understand how a functional network of MPAs should be structured.

We have above explained how marine connectivity can be accounted for in spatial conservation planning, through hydrodynamic modelling, habitat quality maps, and considering species traits, and outlined options available in data pre-processing, during the spatial prioritization analysis itself, and in the post-processing of results. Several broadly similar approaches have previously demonstrated how connectivity can be considered in MPA network planning (Corell et al. 2012; Gallego et al. 2016). Many of these studies have considered oceanographic processes and taken into account dispersal traits, such as typical habitat depth and pelagic larval duration (e.g. Berglund et al. 2012; Corell et al. 2012; Jonsson et al. 2016; Magris et al. 2016), but few have explicitly used

the connectivity data in a multi-criteria analysis that can integrate a broad suite of ecological, economic and societal factors.

Conclusion

Connectivity is important for persistence of marine species that have a pelagic larval phase or other means for passive or semi-passive dispersal. The dispersal rates however vary greatly depending on species traits and geomorphology and oceanography of the sea area in question. In areas where subpopulations occupy isolated habitats and directional currents prevail, connectivity is a major determinant for metapopulation persistence. In contrast in shallow and fragmented areas, where currents are weak and variable, other factors may override the importance of connectivity. We have above discussed the similarities between marine and terrestrial forms of connectivity and demonstrated how partially directed diffuse connectivity can be approximated in the marine environment using a grid-based spatial prioritization tool. While differences in spatial distribution of data layers will be plentiful, we conclude that the same objectives, types of data, methods, analysis structures and connectivity methods are by and large applicable to both terrestrial and marine analyses.

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