Biological Conservation 216 (2017) 93–100

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Perspective

A multiple-species framework for integrating movement processes across life stages into the design of marine protected areas

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ARTICLE INFO

Keywords:
Pelagic larval duration
Home range
Marxan
MPA
Movement
Larval dispersal

ABSTRACT

A major objective of marine protected area (MPA) network design is to ensure the persistence of species with diverse life histories and functional traits. Considering how species differ in their propensity to move within and between MPAs is therefore a key consideration for multi-species MPA network design. Here, we propose a conceptual framework to incorporate ecological processes that affect movement at multiple life stages into the MPA network design process. We illustrate how our framework can be implemented using a set of hypothetical species that represent regional trait diversity in coastal British Columbia, Canada. We focused on two ecological processes: (1) dispersal during the larval phase and (2) daily home range movement during the adult phase. To identify functional connectivity patterns, we used a biophysical model to simulate larval dispersal, and then prioritized highly-connected patches using a reserve selection algorithm. To ensure that individual reserves were commensurate with home ranges, we also imposed reserve size constraints. Candidate areas for protection were identified based on multi-species connectivity patterns and home range size constraints. Collectively, this conceptual framework offers a flexible approach to multi-species, cross-life stage conservation planning, which can be further adapted to address complex life histories. As marine conservation efforts around the globe aim to design ecologically connected networks of protected areas, the integration of movement and connectivity data throughout ontogeny will be a key component of effective multi-species MPA network design.

1. Introduction

Over the past several decades, global monitoring efforts have revealed that marine protected areas (MPAs) have positive effects on both biodiversity and biomass (Claudet et al., 2008; Lester et al., 2009; Edgar et al., 2014). Key characteristics of effective no-take MPAs and MPA networks include large sizes, appropriate spacing, and strong enforcement (Halpern, 2003; Edgar et al., 2014; Gill et al., 2017), yet there is variation in the time lags and magnitude of positive effects (Lester et al., 2009; Molloy et al., 2009). Still, there is much to learn regarding the physical and biological attributes that make MPAs and MPA networks successful.

Variation in ecological and life history traits of species can contribute directly and indirectly to differences in the efficacy of MPA networks. Traits related to mobility, growth, and habitat use have been shown to predict species responses to MPA implementation (Claudet et al., 2010). Additionally, there is evidence that species traits can mediate the positive effects of physical network characteristics. For example, a recent analysis revealed that the positive effect of large MPAs was only observed in certain response variables, such as the biomass of mobile species that frequently swim outside the boundaries of small MPAs (Edgar et al., 2014). Given these lines of empirical evidence, a relevant question becomes: can MPA network optimization be improved by considering species traits more explicitly?

Within an area-based approach to network optimization, species traits related to movement will be among the most straightforward to integrate into network design. Because many marine fishes and invertebrates exhibit a biphasic life cycle that begins with a dispersive larval phase, recent work has begun to address this issue by including dispersal-driven connectivity predictions into network design (Jonsson et al., 2016; Magris et al., 2016; Melià et al., 2016). While larval dispersal is a key driver of connectivity in marine systems, post-settlement

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http://dx.doi.org/10.1016/j.biocon.2017.10.012
Received 19 April 2017; Received in revised form 24 August 2017; Accepted 9 October 2017

Table 1
Examples of ecological processes that result in individuals moving across the seascape. These processes occur at distinct life stages for many marine species.

Life stage	Ecological process	Potential conservation actions	Relevant papers
Larval	Dispersal	● Adjust MPA spacing to ensure connectivity ● Protect areas that are connected hubs ● Protect areas that are self-sustaining	Jonsson et al., 2016; Magris et al., 2016
Juvenile	Ontogenetic migrations	● Protect all habitat types used by different life stages within a population	Mumby, 2006; White, 2015
Adult	Home range movements	● Scale MPA size to species home ranges	Moffitt et al., 2009; Metcalfe et al., 2015
	Seasonal migrations	● Temporary MPAs at seasonal spawning or feeding grounds ● Protection of seasonal migration corridors	Sadovy and Domeier, 2005; Pendoley et al., 2014

ecological processes also play an important role in driving species movement patterns across a seascape (Grüss et al., 2011), and subsequently can affect the demography, distribution, and spread of species (Tamburello and Côté, 2015). An important next step in marine spatial planning is therefore to integrate movement types across life stages for multiple species (Table 1). Examples of post-settlement movement processes include stage-based movements (e.g., individuals moving from foraging to breeding grounds) and ontogenetic migrations, wherein individuals migrate from juvenile nursery habitat to adult habitat (e.g., individuals of many reef species move from mangroves to coral reefs). Previous work has shown that MPA networks may best accommodate species that undergo ontogenetic migrations by ensuring that adjacent patches of nursery and adult habitat are protected (White, 2015). Smaller-scale movements, such as those made by adults within home ranges, can also influence optimal MPA size, since larger protected areas will be needed to minimize the exposure to harvesting of individuals with larger home ranges. In sum, because species have distinct movement patterns at different life stages, the multi-species approach to MPA network design should begin to explicitly consider post-settlement movement for the diverse set of species inhabiting the seascape.

In this perspective, we develop a conceptual framework to optimize MPA networks that accounts for diverse species traits and movement strategies across life stages. We then illustrate how to operationalize this multi-species, cross-life stage framework using a set of hypothetical species situated in coastal British Columbia, Canada. While our perspective focuses on biphasic fishes and invertebrates, the underlying concepts are relevant to a broader suite of marine taxa, such as cetaceans, sea birds, and turtles.

2. Conceptual framework

Following the conceptual framework diagram (Fig. 1), we outline steps to design a multi-species MPA network that accounts for cross-life stage movement of a set of target species. Here, target species may represent a set of commercially important species that the network aims to protect. Alternatively, it may represent a suite of co-occurring species that represent regional life history diversity. We focus on four key steps.

2.1. Larval dispersal and connectivity

Larval dispersal is notoriously difficult to measure directly. In some cases, direct dispersal data (e.g., mean dispersal distance) may be available from genetic parentage studies (D'Aloia et al., 2015; Almany et al., 2017) or otolith tagging (Jones et al., 2005). More frequently, larval traits are used to predict dispersal using biophysical transport models. Once dispersal is measured or predicted for multiple species, a common next step is to combine single-species connectivity data into multi-species connectivity metrics (e.g., centrality, in-flux, and out-flux) to capture the variation in connectivity patterns that exists within ecological communities (Jonsson et al., 2016; Magris et al., 2016; Melià et al., 2016). These multi-species connectivity metrics are used as inputs into the MPA selection algorithm.

2.2. Ontogenetic migration from juvenile to adult habitat

If species in the study area undergo ontogenetic migrations, and the populations are subject to harvesting or other anthropocentric activities during both the juvenile and adult stages, it may be necessary to protect both habitat types (White, 2015). In an area-based approach to network optimization, this can be achieved by creating a 'cost' to the reserve network if both habitat types are not included in the network (Beger et al., 2010).

2.3. Adult migrations and home range sizes

Additional adult migration events may occur later in life that also warrant protection. For example, adults of some marine species undergo seasonal migrations to form spawning aggregations (Domeier and Colin, 1997), where they are particularly susceptible to overfishing (Sadovy and Domeier, 2005). The locations of spawning aggregations or spawning grounds for a set of exploited focal species are strong candidates for temporary protection in the MPA network. Similarly, other species may undergo seasonal migrations to feeding grounds, or, at higher latitudes, to overwintering habitat (Hay, 1985; Rose, 1993). Insofar as these seasonal habitat uses are located in geographically-defined space, occur at predictable times, and expose populations to harvesting pressures, these areas may also be strong candidates for temporary protection. Daily adult movements have also long been recognized as important to MPA design (Moffitt et al., 2009). Specifically, home range size, defined as the primary area where an adult individual engages in daily activities, can influence the minimum reserve size needed to ensure that most individuals stay within MPA boundaries. In a multi-species context, the minimum reserve size may be constrained by the largest home range for a set of focal species that occupy a given area. Recent advances in marine spatial planning tools allow any prospective MPA to be modified with minimum size constraints that reflect home range sizes (Smith et al., 2010).

2.4. Reserve network optimization

All of this information about how species move across the seascape, at different life stages, is fed directly into the optimization process. By considering how species use space over time, this multi-species, cross-life stage framework can aid the design of networks that protect connectivity and reduce overharvesting post-settlement. While the ecological processes we present here are not exhaustive, they represent a range of movement types that occur throughout marine species' ontogeny. This framework could be further adapted to include additional processes, based on the seascape and species of interest. In practice, all of these considerations must be incorporated into multi-objective, regional conservation plans that also consider socio-economic and cultural objectives, and additional biological or physical data.

3. Case study: a simulation of hypothetical species

We applied our conceptual framework to a set of hypothetical species situated in the northeast Pacific Ocean along the coast of British