



Dispersal connectivity and reserve selection for marine conservation

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ABSTRACT

Although larval dispersal is crucial for the persistence of most marine populations, dispersal connectivity between sites is rarely considered in designing marine protected area networks. In particular the role of structural characteristics (known as topology) for the network of larval dispersal routes in the conservation of metapopulations has not been addressed. To determine reserve site configurations that provide highest persistence values with respect to their connectivity characteristics, we model nine connectivity topological models derived from graph theory in a demographic metapopulation model. We identify reserve site configurations that provide the highest persistence values for each of the metapopulation connectivity models. Except for the minimally connected and fully connected populations, we observed two general ‘rules of thumb’ for optimising the mean life time for all topological models: firstly place the majority of reserves, so that they are neighbours of each other, on the sites where the number of connections between the populations is highest (hub), secondly when the reserves have occupied the majority of the vertices in the hub, then select another area of high connectivity and repeat. If there are no suitable hubs remaining then distribute the remaining reserves to isolated locations optimising contact with non-reserved sites.

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1. Introduction

In recognition of the interconnectedness of marine systems, increasing emphasis has been placed on establishing ecologically connected networks of protected areas as a pragmatic solution to the conservation of insufficient habitat area (Sala et al., 2002; Mora et al., 2006; Jones et al., 2007, 2009). As the populations of most marine species exchange juvenile organisms between sites (defined as discrete seascape features such as a coral reefs) for recruitment (Botsford et al., 2001), small isolated marine protected areas (MPAs) are unlikely to ensure the persistence of marine metapopulations (Mora et al., 2006). Instead, networks of MPAs that reflect the inter-site connectivity are required to ensure that the processes supporting marine populations are adequately incor-

porated in marine conservation efforts (Mora et al., 2006; Jones et al., 2007; Kaplan et al., 2009). This paper provides a theoretical framework to integrate complex patterns of dispersal connectivity systematically into marine conservation planning. To do this we first describe nine connectivity patterns. Then we use a greedy algorithm to find the best reserve system design, based on maximising the metapopulation persistence, for each pattern given a constraint on how much of the system can be reserved.

Many definitions of structural, potential and actual connectivity have been identified and discussed in the ecological literature (Bridgewater, 1987; Taylor et al., 1993; Schumaker, 1996; Fall et al., 2007; Minor and Urban, 2008, 2010). In this paper, we focus on intergenerational dispersal among discrete habitat sites, such as found in many marine plants, invertebrates and fishes, where the net movements of larval propagules among habitat sites are significantly greater than those of relatively sedentary adult stages (Grantham et al., 2003). The role of environmental stochasticity, larval mortality and fecundity fluctuations (Hughes et al., 2000; Knights et al., 2006; Graham et al., 2008) can influence the long term flow of viable recruits however the connectivity regime utilised in

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this paper is based on the fixed proportion of the yearly cohort that will depart from a natal site and arrive at a settlement site. For the model presented here, the magnitude of connectivity is determined by the probability of larval dispersal success combined with the population fecundity and environmental stochasticity of the source and settlement sites. The magnitude and the structure of the connections define the metapopulation character (Kritzer and Sale, 2004).

Many species exist as metapopulations because of the fundamental patchiness of the natural world, the specificity of their habitat requirements and their movements among these sites (Hanski, 1994; Lewis, 1997; Bascompte et al., 2002). Marine populations particularly depend on dispersal dynamics given their reliance on patchy habitats (e.g. estuaries, rocky pinnacles, kelp forests and coral reefs) and their long-lived and potentially long-distance dispersing planktonic larvae (Grantham et al., 2003; Kinlan and Gaines, 2003; Treml et al., 2008). Despite increasing attention on the proportion of marine larvae that “self-recruit” back to the same population as their parents (Jones et al., 1999, 2005; Hastings and Botsford, 2006a; Almany et al., 2007), most marine populations are still considered to be influenced by recruits from elsewhere (Underwood et al., 2007; van Oppen et al., 2008).

Despite this emergence of connectivity research, the sensitivity of marine populations to marine dispersal processes is rarely systematically considered in marine conservation planning (Cerdeira et al., 2005; Sale et al., 2005). This is not withstanding the growing collection of research publications that are *evaluating* MPA networks (see review by Pelletier and Mahevas, 2005). Linear reserve systems along a variable coastline (Walters et al., 2007; Kaplan et al., 2009), single species models within a heterogeneous two dimensional habitat (Kraus et al., 2008) and multi-species models (Mahevas and Pelletier, 2004; Yemane et al., 2008) all incorporate complex life cycle information to estimate fish abundance trajectories within a MPA network. Several models also include spatially explicit sub-models of fishing effort and resource management (ISIS-Fish model, Mahevas and Pelletier, 2004; Kaplan et al., 2009). In contrast the model proposed here seeks to develop the foundations for conservation planning that incorporate connectivity by offering a simpler metapopulation model within a more complex network structure. As such our model advances the linear dispersal work by Kaplan et al. (2009) to large complex two dimensional site configurations and connectivity patterns.

Conservation planning often ignores the patterns but instead focuses on the importance of protecting “source” over “sink” populations (Crowder et al., 2000). Yet protecting a set of highly productive, but disconnected, sources could be worse than protecting a well connected chain of lesser sources, as the overall strength of the connections within the network is important for metapopulation persistence (Tuck and Possingham, 2000; Bode et al., 2008; Beger et al., 2010). The key to metapopulation persistence is the combination of source strength and whole system connectivity. The trade-off of a site’s demographic output and its connections within the MPA network remains a challenge to conservation planners (Almany et al., 2009; Hodgson et al., 2009).

Contemporary conservation planning methods tend to be based on biodiversity patterns (Cerdeira et al., 2005; Roberts et al., 2006; Fernandes et al., 2009), and largely ignore dynamic processes (Pressey et al., 2007; Moilanen et al., 2009). Connectivity patterns between marine habitats do not necessarily represent spatial biodiversity patterns (Sala et al., 2002), with high variability often observed among the systems studied (see GBR example; Pitcher et al., 2007). Depending on oceanographic and atmospheric circumstances, larval characteristics and behaviour, and scale, any spatial arrangement of sites could have many different patterns of connectivity (Byers and Pringle, 2006).

The structure of connectivity models and their implications for conservation planning are largely determined by spatial scale and are often species-specific (Shanks et al., 2003). For example, a species with long-lived larvae and long dispersal distances, will require large scale management to influence the larval recruitment (Botsford et al., 2006). At smaller scales, only species with short dispersal capabilities will be influenced by connected MPA networks (Hastings and Botsford, 2006a; Kaplan et al., 2009).

Complex larval dispersal networks are not randomly structured but instead have a topology based on their functional characteristics (Minor and Urban, 2008). In this context ‘topology’ is the term describing structural characteristics of a network (Albert and Barabasi, 2002) that remains despite being deformed. For example a lattice structure with a regular pattern of four connected vertices will retain a lattice topology despite being twisted or stretched. Certain topologies can create modules, or highly connected regions, known as hubs. The definition of a ‘hub’ is difficult to specify exactly. In graph theory, determining the modularity or community structure of networks is a theoretically challenging exercise (Porter et al., 2009). Just identifying the vertices with the highest number of connections is often insufficient to determine the modular structure (Li et al., 2005). Algorithms that attempt to split a network into a series of structural units, are based on a heuristic mechanism that seeks to formalise the basis of what constitutes a ‘good’ community (Newman, 2006; Leicht and Newman, 2008; Butts, 2009).

In this paper we present a comprehensive array of dispersal connectivity topologies that affect strategies for conservation planning. In this conservation framework, whether a site is allocated reserve status, or not, implies the influence of fishing pressure and directly changes the local extinction rate within the metapopulation model. Importantly the model presented does not directly address fisheries based issues of spill over and sustainable yield. More detailed modelling regarding specific fish stock management (Kaplan et al., 2009) would be required to make this model applicable to fisheries management.

2. Materials and methods

Here we do not attempt to represent arbitrary patterns of metapopulation connectivity, nor do we develop patterns specific to a particular system. Rather, we examine a representative set of topologies that capture some of the most commonly evoked patterns of connectivity so as to demonstrate our method and understand its basic functioning.

Our taxonomy of connectivity classifies the myriad different possible connectivity patterns into nine “connectivity topological models” that represent recognisable types of distinct connectivity (described in Table 1, Fig. 1), and discusses differences in conservation. The connectivity topological models include the (1) minimally connected, (2) larval pool with equal redistribution (LPER), (3) nearest neighbour, (4) small-world, (5) linear, (6) tree, (7) minimum fixed distance (geometric), (8) random network and (9) scale free.

To evaluate the quality of reserve networks within the different connectivity topological models, we used the expected mean life time (MLT) of a metapopulation (Drechsler, 2009; Kininmonth et al., 2010b). A fixed number of pelagic offspring disperse and recruit to sites to which they are connected (including their natal site) each year within the stochastic metapopulation model. We assume the connectivity patterns are constant from year to year although in general connectivity patterns vary between years (Siegel et al., 2003; Bode et al., 2006; Treml et al., 2008). The complexity of larval dispersal connectivity is incorporated into our metapopulation model with the use of a *graph-theoretical network*, a data object that stores all the relevant information about the outcome of a dispersal process (see example at Kininmonth et al.,

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