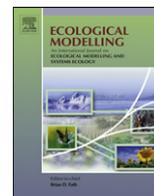




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Dispersal connectivity and reserve selection for marine conservation

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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; Trembl 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; Trembl 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.,

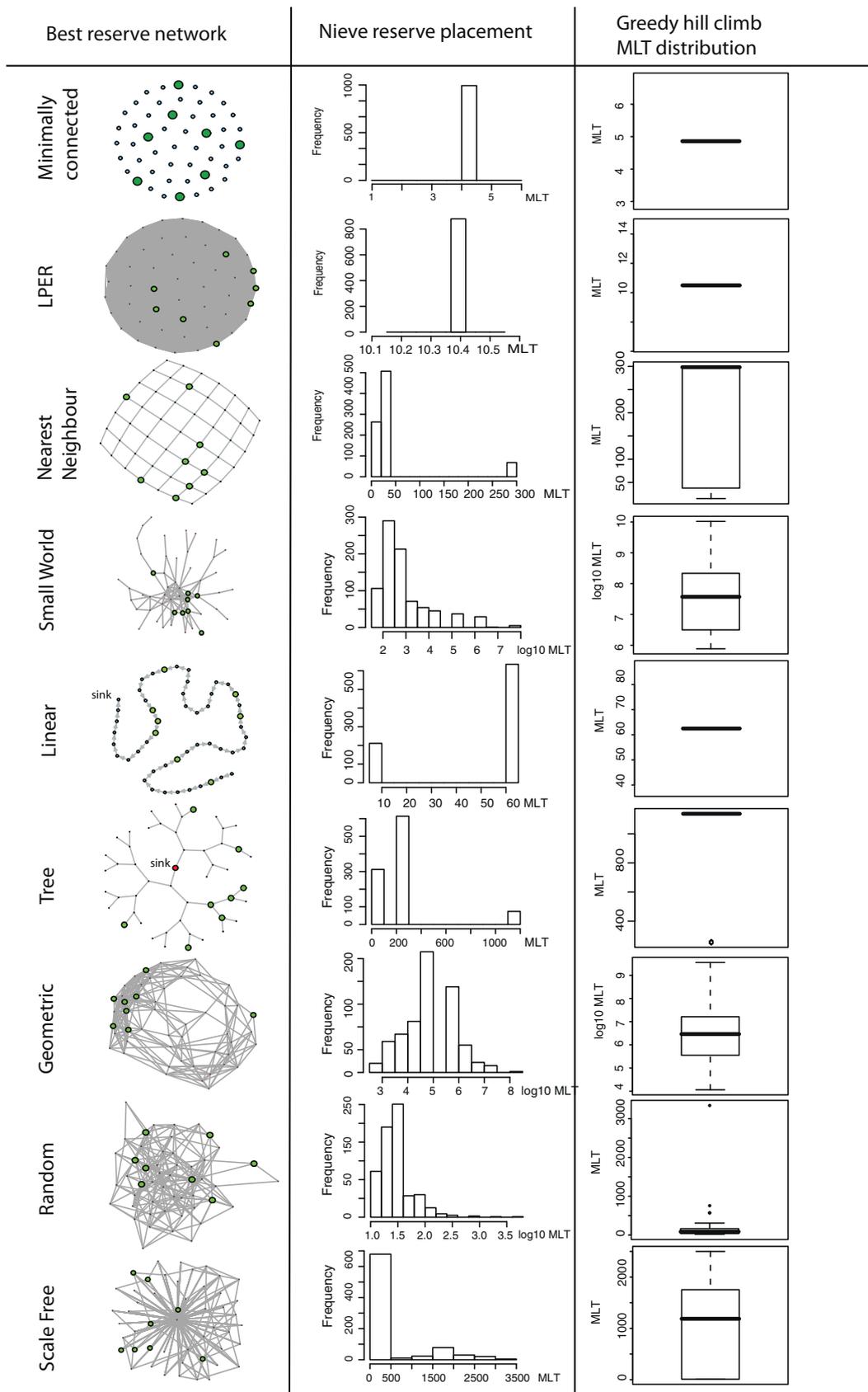


Fig. 1. Topological models and MLT distributions. The first column presents the best reserve configuration determined by the hill climb algorithm. The larger green circles are the 8 reserves for each of the topologies described in Table 1. The second column is the histograms of the random placement of reserves for 1000 iterations. The third column contains boxplots of the MLT values generated from 100 iterations of the stochastic hill climb greedy algorithm.

Table 1
 Alternative networks for comparison (see Fig. 1).

Model name	Description
Minimally connected	Technically this is not a network but to make the comparison work the LPER network is used with the edge weights set to a very low value. This effectively makes the connections potentially available but presently non-functional.
LPER	This graph has every node connected to every other node. (Csardi and Nepusz, 2006)
Nearest neighbour	This pattern is represented by a lattice of 2 dimensions composed of a set of four vertices joined in a square (Csardi and Nepusz, 2006).
Small World	Using the Forest fire algorithm this network model resembles how a forest fire spreads by igniting trees close by (Leskovec et al., 2007). Vertices are added sequentially and edges are created with respect to the neighbouring configuration.
Linear	This model is based on a simple single connection between each neighbour. The direction of the edges is set to flow from one end to the other end of the network like a coastal flow (Csardi and Nepusz, 2006).
Tree	This model is based on a regular tree with 2 edges connecting the 'child' neighbours. The direction of the edges are set to flow from child to parent vertices like a river network (Csardi and Nepusz, 2006). The central vertex is the final destination or 'sink' of this flow model.
Geometric	First a number of points are dropped on to a unit square, then two points will be connected with an undirected edge if they are closer to each other in Euclidean norm than a given radius (Csardi and Nepusz, 2006).
Random	Initially the vertices are created then the set number of edges (4 times the vertex number in this paper) are allocated randomly (Erdos and Renyi, 1959).
Scale Free	We use the Barabasi–Albert model whereby one vertex is added in each time step and edges are then created to link existing vertices with a scale free probability, $P(k) \sim k^{-\gamma}$ (Barabasi and Albert, 1999).

2010a). We can define this graph $G(V,E)$ as a finite set of vertices V , connected by edges E . The degree (k_i) of a vertex i defines the number of connecting edges and hence the number of neighbouring vertices. The average degree for all the vertices in a graph is denoted as $\langle k \rangle$. The clustering coefficient (CI), as defined by Montoya and Sole (2002), is the sum of the number of triangular linkages $\vartheta_i (i \in V_1, \dots, V_n)$ within the set of neighbours for a selected vertex divided by the maximum possible neighbour linkages where n is the number of vertices in the network. The average minimum path length L is the average number of edges in the shortest path $L_{Min}(i,j)$ between all pairs $V(i,j)$ in a graph averaged over $n(n-1)/2$ vertices (Montoya and Sole, 2002). The diameter, D , is the longest minimum path length that exists between any vertices in a network.

Each vertex i has the attribute of area (A_i) and each edge, E_{ij} , has a weight (w_{ij}) indicating the strength of connection between two populations (i and j). The weight (w_{ij}) represents the proportion of larvae produced at site i that disperse to site j .

Following Drechsler (2009) and Frank and Wissel (2002) the local populations have a local extinction rate

$$v_i = \varepsilon A_i^{-\eta} \quad (1)$$

where ε is a species-specific coefficient relating to minimum site size, and η is the extinction–area exponent. A smaller value of η indicates a strong environmental variation and consequently a slow decline of local extinction rates to area. As described in Kininmonth et al. (2010b) the summation of the outbound edge weights (w_{ij}) for each vertex (referred to as vertex strength s_i^{out}) is used to measure

the emigration rate;

$$n_i^{out} = s_i^{out} = \sum_{j \in v(i)} w_{ij} \quad (2)$$

The rate at which a site i is colonised is

$$u_i^{in} = \frac{1}{\mu} \sum_{j \in v(i)} \frac{w_{ji}}{v_j} \quad (3)$$

where μ is the colonisation number indicating the number of successful recruits needed to restart a colony and v_j is the extinction rate of each neighbour of V_i . The colonisation strength of each site is given by

$$u_i^{out} = \frac{1}{\mu v_i} \sum_{j \in v(i)} w_{ij} \quad (4)$$

which is essentially a measure of the dispersal capacity of the neighbouring sites. Next we calculate the colonisation–extinction ratio for each site using the harmonic mean of Eqs. (3) and (4) (Drechsler, 2009, Eq. (8)). The aggregated geometric mean of the colonisation–extinction ratio (Drechsler, 2009, Eq. (9)) for the entire network, q , is then combined with the geometric mean of the local extinction rates, v (Drechsler, 2009, Eq. (10)), to calculate the approximate mean life time of the entire metapopulation (consisting of N populations) by the formulae (Drechsler, 2009)

$$MLT = \frac{1}{v} \sum_{i=1}^N \sum_{k=i}^N \frac{1}{k} \left(\frac{(N-i)!}{(N-k)!} \right) \frac{1}{(N-1)^{k-i}} q^{k-i}. \quad (5)$$

2.1. Selection of optimal MPA systems

We model the optimisation of the MPA network configuration in 4 steps, in R (<http://cran.r-project.org/>) using the igraph package (Csardi and Nepusz, 2006).

2.1.1. Step 1: create a graph defining the topological model and generate connection strengths

For each topological model we generate a network of a set size (50 vertices) with the algorithms listed in Table 1. We then calculate the weight for each edge based on a total weight value (1500) divided by the number of edges which varied for each topology (see Table 2). Following the findings of Underwood et al. (2007) that the majority of *Seriatopora hystrix* larvae settle within 100 m of their natal colony we set the area value at 2 ha. Exploration of MLT values for the η and ε parameter space indicated the parameter values with sufficient variation and acceptable ranges: $0.01 < \eta < 4$, $1 < \varepsilon < 100$. We then chose a rather small value of $\eta = 0.1$ which represents weak environmental stochasticity (Drechsler, 2009). The species-specific coefficient ε was set in the middle of the acceptable range to 45.

The value of the minimum number of immigrants required (μ) was set at 2. All the parameters established above are designed to maintain the MLT values at realistic values given the area parameterisation.

2.1.2. Step 2: allocate randomly 16% of sites as reserves and adjust extinction rate

Recent marine reserve design and implementation efforts achieved between 5 and 33% reservation of habitats (Day et al., 2003; Mora et al., 2006) so we conducted our analyses with a 16% MPA network. Our approach to defining the influence of a reserve is to increase the extinction–area parameter η value. A random selection of 8 sites was 'protected' by changing their η values to 1.5 (from 0.1).

Table 2

Results of the simulations showing edge number (E), average degree ($\langle k \rangle$), Cluster Coefficient (CI), average minimum path length (L), longest diameter (D), random placement minimum, maximum and mean MLT values and the hill climb MLT minimum, maximum and mean values.

Topology	E	$\langle k \rangle$	CI	L	D	MLT (min, max, mean)	
						Random placement	Hill climb algorithm
Minimal	2450	0	0	0	∞	4.8, 4.8, 4.8	4.8, 4.8, 4.8
LPER	2450	98	1.0	1	1	10.4, 10.4, 10.4	10.4, 10.4, 10.4
Nearest neighbour	84	3.4	0	4.2	12	10.1, 298.3, 50.9	15.1, 298.3, 208.8
Small World	119	4.7	0.4	1.8	5	45, 4.0×10^7 , 2.9×10^5	59.0, 1.0×10^{10} , 2.6×10^8
Linear	49	1.9	0	17	49	8.8, 62.4, 49.1	62.4, 62.4, 62.4
Tree	49	1.9	0	2.6	5	24.8, 1137.9, 255.3	255.5, 1138.0, 890.9
Geometric	264	10.56	0.6	2.3	5	340, 1.2×10^8 , 1.0×10^6	11500, 3.5×10^9 , 7.5×10^7
Random	200	8.0	0.1	2.8	7	10.7, 4458.0, 48.0	18.0, 3339.0, 184.0
Scale free	343	13.72	0.1	1.2	3	9.3, 3481.0, 414.3	9.3, 2499.0, 979.1

2.1.3. Step 3: calculate persistence value

We calculated the metapopulation mean life time (MLT) of the network with its reserve system using Eq. (5).

2.1.4. Step 4: find a network with high persistence

We used an iterative algorithm to find an approximate optimum of reserve sites placements given the objective of maximising metapopulation mean life time. To find a good reserve system we used a hill climbing algorithm. Hill climbing algorithms start with a random solution (e.g. allocation of sites as reserves) and a small change is made (e.g. randomly switch one non-reserve with a reserve). The resultant solution is then compared to the current solution (using the MLT values). If the new solution is better than the previous solution then the new solution is retained while the older solution is discarded. This process is repeated until no more improvements can be found given a set number of iterations.

This simulation was repeated 100 times using the same network but with different random initial reserve placements. The hill climb algorithm only finds a local optimum and so the best reserve network from the 100 iterations was retained as an example.

2.2. Naive reserve placement

To replicate the scenario where reserves are placed without knowledge of the connectivity processes we created randomly allocated reserves and measured the MLT (steps 1–4 only) for 1000 independent instances of each topological model.

2.3. Increase reserve percentage

We also examined the change in MLT values for each topological type as the percentage of reserves was increased from 20% to 80% in 5% increments, for a 50 site network. Each network model was optimised using the hill climb algorithm.

2.4. Edge weight, network size and site area sensitivity simulation

The responses of the model presented here to situations such as the placement of reserves in systems that are very weakly connected or that have changes in site area or changes in the number of connected sites were explored. The total edge weight value was stepped through from 1 to 14,001, in 1000 increments, while examining the optimal reserve placement. Similarly the site area was changed from 0.2 to 24.2 and the site number from 20 to 100 while examining the MLT values and the reserve placement.

3. Results

The 9 topologically different networks (Table 1, Fig. 1), with 50 sites including 8 reserves, had MLT values ranging from 4.8 (minimally connected) to 3.5×10^9 (geometric) years. The results for each topological model are different and described in detail

in Table 2 and summarized in the following. For the minimally connected model the randomly placed reserves all had the same value and this result was reflected in the single MLT value derived from 100 iterations of the hill climb algorithm. The LPER (fully connected) model showed that changes in reserve placement did not change the MLT values.

For the nearest neighbour model the hill climb algorithm was able to optimise the reserve allocation in 60% of simulations so that the MLT value was at the maximum value. The best reserve placement for the nearest neighbour model was to place three or more reserves closely connected to each other and the remaining reserves distributed in pairs or singularly around the network.

The small world model generated MLT values that were significantly improved by the hill climb algorithm. The reserve placement in the best reserve network allocated the majority (6 out of 8) of reserves to the densely connected regions of the network and a minority in more isolated sites. For the linear model random reserve placement generated two values which can be attributed to a small number of reserves being placed adjacent along the linear network. The hill climb algorithm reflected this with a single optimal MLT value.

The tree model found that the hill climb algorithm was able to improve the majority (84%) of best reserve networks. The placement of 4 reserves in a group on one tree branch with the remainder placed at the starting locations on separate branches generated consistently high MLT values.

The geometric or minimum fixed distance model demonstrated increased MLT values following the placement of reserves using the hill climb algorithm. Reserves placed within the highly connected regions of the geometric network with only a minority placed in more isolated regions generated the highest MLT values.

The random model did not respond, in general, with higher MLT values due to the placement of reserves through a hill climb algorithm. The optimisation algorithm relies on random changes selecting sites with higher connectivity which is an improbable task for this topology.

The scale free model has a degree distribution (based on $P(k) \approx k^{-\gamma}$) that results in a small number of vertices having a very large number of connections. The randomly placed reserves generated a bimodal MLT distribution while the hill climb algorithm only increased the MLT distribution marginally. The hill climb algorithm did not change the bimodal structure of the distribution and, with only minor change in the mean values, this algorithm did not prove suitable for scale free networks.

The increase in the reserved percentage from 20 to 80% for a 50 vertex network based on each topological style generated MLT values ranging from 5.1 to 3.3×10^{11} (Fig. 2). All the topologies, except the geometric, random and small world, exhibit a linear increase in MLT for a change in the percentage of reserves. For the geometric, random and small world networks the increase in reserves generated a logarithmic change in MLT. An example of the changes in the

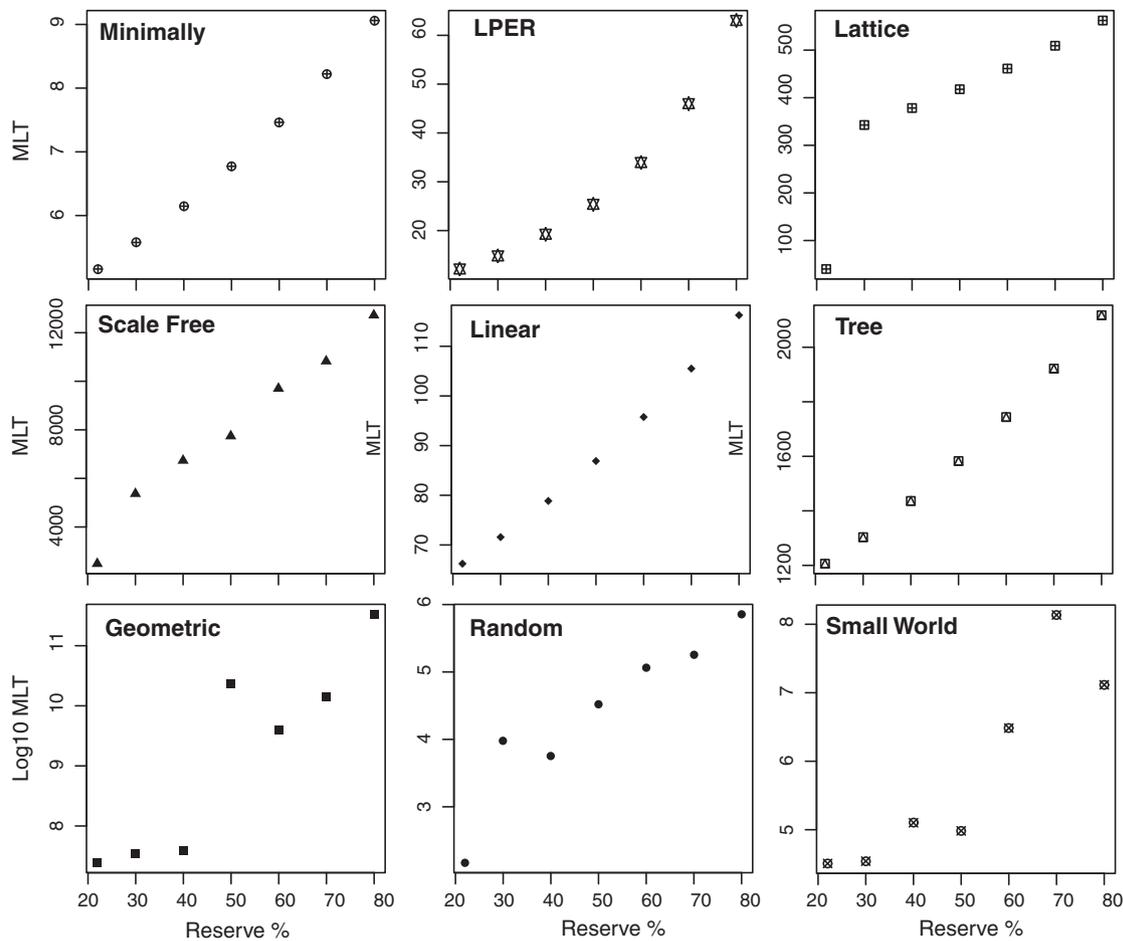


Fig. 2. Changes in MLT (log₁₀ MLT for geometric, random and small world) for increases in the percentage of reserves across the range of topologies. Each point within the graph represents a locally optimised reserve network of 50 vertices.

reserve placement is provided in Fig. 3 which for graphical purposes uses a larger 100 vertex geometric network. The thicker lines in Fig. 3 are those edges that radiate out from the reserves highlighting the extent of the influence of the reserves. The early placement of reserves in the highest connected region of the network is evident followed by the placement of reserves in more isolated locations.

Changing the edge weight, site area and network size values resulted in a logarithmic change in the MLT for the scale-free, small world and geometric network topologies (Fig. 4). Specifically the scale free networks showed the highest variability for weight and area changes. This was expected since the hill climbing algorithm did not specifically target highly connected sites for reserve allocation and hence these highly influential sites frequently missed out. The small world topology responded with the smallest increase in MLT following an increase in network size. The geometric topology increased the MLT values consistently across all three parameter changes. Observations of the network placement for the different topologies and across the three parameter changes showed that the optimal MLT values were achieved by initially placing the reserves into the regions of highest connectivity then allocating reserves in more isolated sections of the network. However, when the total edge weight was less than 1000 or the site area was less than 0.3 Ha, the reserves were allocated randomly rather than targeting the hubs.

4. Discussion

Our metapopulation modelling within nine connectivity topological models demonstrates that selecting reserve sites with

consideration of connectivity increases the persistence of metapopulations unless there is minimal connectivity or every site is equally connected. For populations of sessile adults with significant larval dispersal stages we propose a simple two part guide that will help establish a theoretical framework for conservation planning with respect to topology:

- (1) initially place reserves, so that they are neighbours of each other, within the region with maximum connection density (hub),
- (2) when the reserves have occupied the majority of highly connected sites within this hub then select another hub and repeat. If there are no suitable hubs remaining then distribute the remaining reserves to optimise contact with non-reserved sites.

The nine topological models described here also exhibit individual characteristics for the optimal placement of reserves and thus the knowledge of the connectivity patterns is useful for marine reserve planners. However we acknowledge that the simplicity of these models will ignore the more complex connectivity functions observed in marine systems and in particular the protection of ‘stepping stones’ and isolated clusters are not directly embraced by this modelling approach. We also emphasize that the metapopulation model used in this reserve optimisation model is limited and does not include trophic interactions, rescue effects, density dependent selection or demographic influences. For each pattern we discuss the unique results and implications for conservation planning.

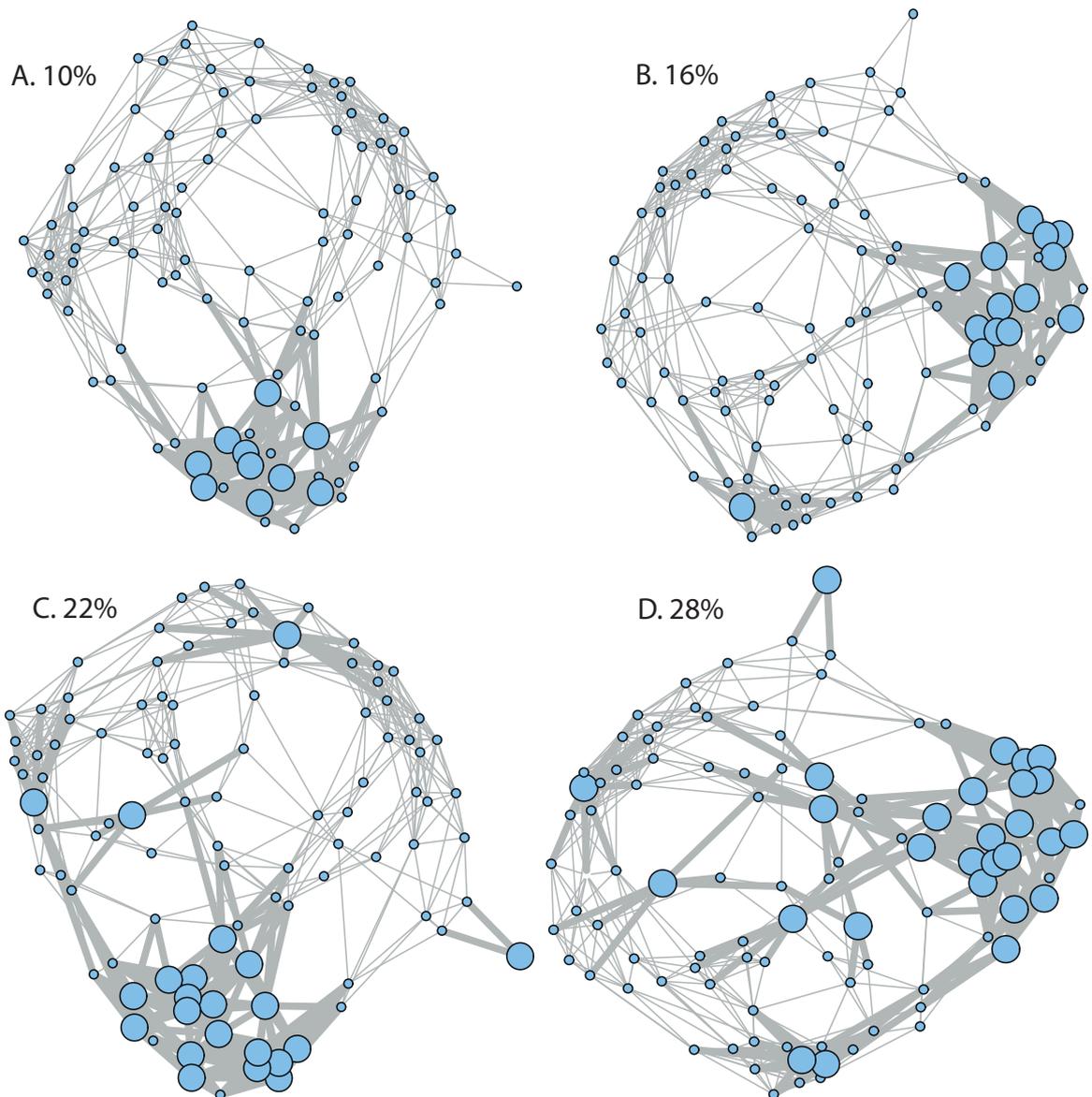


Fig. 3. Placement of reserves (larger circles) given the increase in the percentage of vertices protected. Each network was based on a single instantiation of the Geometric topology with 100 vertices showing the 10, 16, 22, 28% reserve placement. Each final network was optimised by the hill climb algorithm. The thicker lines radiating from the reserves indicate the immediate connections and the sphere of influence.

4.1. Minimally connected pattern

When there is minimal dispersal between sites or where no information on dispersal exists, connectivity cannot improve the planning of a MPA network. As the persistence of the metapopulation is not reliant on connectivity (each population must be persistent on its own as there is no dispersal), planning objectives may follow general guidelines of planning for comprehensiveness, adequacy and representativeness (CAR) for each population separately (Stewart and Possingham, 2003).

4.2. LPER connectivity pattern

If all sites are equally connected to each other, then any site in the system will receive larvae from all the remaining sites. Thus, all MPA network configurations with LPER topology will result in the same connectivity outcome and connectivity can be discarded as a factor that informs reserve design. Conservation planning may pro-

ceed following the basic CAR objectives (Stewart and Possingham, 2003).

4.3. Nearest neighbour connectivity pattern

In the nearest neighbour pattern, our model suggests that persistence was best achieved by forming a 4 or more reserve cluster (direct connection between reserves) with those vertices that were not on the boundary (limited to 3 edges) and then distributing the remaining reserves around the network (Fig. 1). By protecting the process of recruitment in one part of the seascape, we created a long term source of larval supply for the remaining unprotected sites. Mora et al. (2006) promote the conservation design concept that marine reserves should be located as a linked sub-network based on the dispersal distances. In graph theoretic terms this concept can be described by a minimum spanning tree where a connected string of reserve vertices spans the network connecting to the maximum number of non-reserved vertices (Fall et al., 2007). The percentage of reserves required to complete such a design would depend on

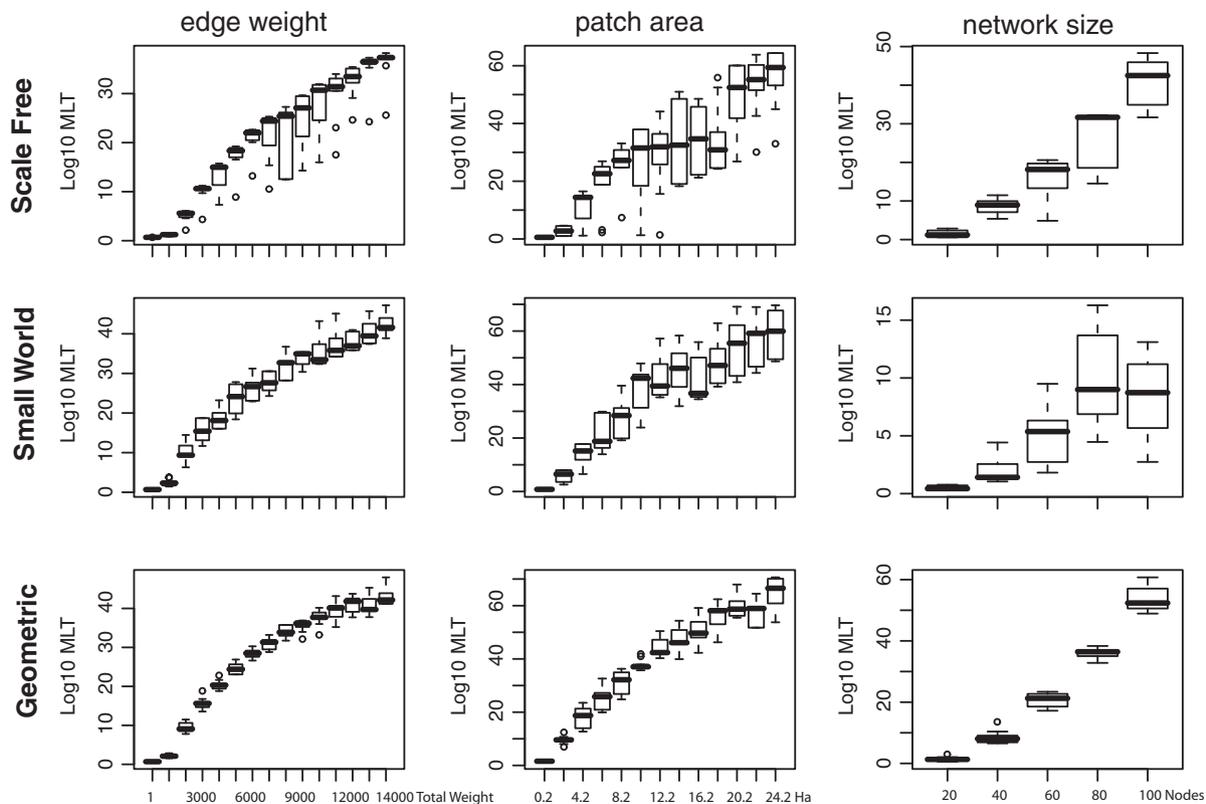


Fig. 4. Changes in the MLT values as the values of the edge weight, site area and network size was changed for the scale free, small world and geometric topologies. The percentage of reserves was 16%.

the topology but will necessarily be high in a Nearest Neighbour network due to the maximum degree of 4.

4.4. Small-world connectivity pattern

For the small-world topological model it is crucial to protect the hubs, however, rather than reserving all the hubs evenly, our model supports the initial placement of reserves in a single region dominating a single hub. This means that conservation planning should proceed by identifying and protecting a significant proportion of sites located within hubs within small world networks. [Visconti and Elkin \(2009\)](#) also found aggregated sites (hubs) generated higher persistence within their metapopulation modelling than populations located evenly across the landscape. They also included the quality of the site in their model and found that variable quality across the landscape was more persistent than aggregated high quality simulations. While our model has an initial uniform quality (expressed as the extinction-area exponent η) the reserve allocation process (reduced extinction rate) has the effect of increasing the capacity of a local population to persist. Again in agreement with [Visconti and Elkin \(2009\)](#) our model placed reserves that were excess to the domination of the hub sites, in a distributed fashion across the sites.

4.5. Linear connectivity pattern

In this scenario, downstream sites receive a quantity of settling larvae from upstream sites; hence it is intuitive that these upstream sites that should be an MPA priority akin to freshwater conservation planning. However our results consistently indicate an alternative strategy of initially placing (approximately 3) reserves grouped together with the remaining reserves distributed evenly along the network.

4.6. Tree connectivity pattern

The tree model simply joins at each ‘child’ site eventually flowing all the larvae into a single ‘sink’ site. Given the catchment of larvae generated by the branching structure it is intuitive that upstream sites that should be reservation priority. However our results consistently indicate an alternative strategy of initially placing reserves grouped together on one branch with the remaining reserves placed at the head of each branch. The conservation planner will need to carefully examine the scale of the seascape network to determine if each ‘stream’ should be treated as independent.

4.7. Geometric network

Geometric networks reflect the classic dispersal over a radiating distance (up to a distance threshold). The connections often form local clusters and the distribution of connections is heterogeneous across the network. The results here are similar to the Small World topology with clusters of reserves dominating the higher connected regions to form the best reserve network.

4.8. Random network

For this scenario the connections between sites are randomly allocated with an average degree of 8. In a similar manner to the small world and geometric networks the placement of reserves should target the highest connected regions. If these regions cannot be identified then planners should consider the homogeneous network in a similar way to the Nearest Neighbour topology. The principal design issue here is the random or transient nature of the connections. If the situation exists that the dispersal processes randomly change then the conservation planning will need to develop a flexible approach or accept the sporadic nature of connections

and increase the reserve area to compensate. Kininmonth et al. (2010a) found the dispersal network structure of the Great Barrier Reef changed every year but the stronger connections were highly likely to remain in place. Weaker long distance connections are necessarily unreliable but still important to the long term gene pool (Underwood et al., 2007; van Oppen et al., 2008).

4.9. Scale free network

This network has a small number of vertices that are highly connected and our model identified these sites for protection first to maximise the persistence. The importance of scale-free architecture on network function is a matter of recent research (Li et al., 2005; Barabasi, 2009). The spread of disease within scale free networks (Dezso and Barabasi, 2002; Pastor-Satorras and Vespignani, 2002) has shown that the highest connected vertices are not necessarily the principal infection agents. Rather, as Li et al. (2005) highlights, understanding the critical topology for the highest connected vertices is essential to unlocking the key to network function. The hub structure that controls the majority of linkages is the key to understanding the dispersal across a scale-free network.

Interestingly the solutions for the various connectivity topological models appear similar (Fig. 1); the best MPA networks always included some clusters of reserves centred on the highest internal connections. Exploring this reserve allocation process further we examined the incremental changes in reserve design following increases in the percentage of reserved vertices (Fig. 2). The hill climb algorithm did not simply select the vertices with the highest ranking number of connections. Instead the reserve allocation was a more complicated arrangement with reserves initially being placed together in order to dominate a hub followed by dispersal throughout the network. The optimisation algorithm evaluates whether an additional reserve is best placed in a hub (where it can 'support' both existing reserves and non-reserves) or in a region of lesser connection density in order to optimise the persistence value.

Our metapopulation algorithm, within the parameter space we selected, clearly favoured the notion that the dispersal feedback loop created between closely connected reserves results in a longer overall persistence than evenly distributing the reserves across the network. Kaplan et al. (2009) also found that for long distance dispersers a cluster of marine reserves increased the settlement of the juveniles inside and outside the reserve areas. However no other studies have identified the second step of the allocation process, namely the placement of reserves in remote locations once the hubs have been dominated. Ensuring the spatial pattern of reserves align with the dispersal characteristics and metapopulation dynamics of the target species is fundamental to long-term metapopulation persistence (Yemane et al., 2008).

Does this phenomenon of protecting the hubs with a dominating set of reserves in order to optimise the metapopulation persistence apply for systems that vary in the number of sites, the size of the sites or that are predominantly self recruiting? Our results (Fig. 4) show that when the colonisation rate is very low (due to small site area or low connectivity) that the topology of the reduced dispersal network is not influential in determining the prioritisation of reserve allocation. In other words, for the networks that are reduced to a minimally connected system conservation planning should instead focus on the CAR principles (Stewart and Possingham, 2003). In contrast the size of the network within this modelling framework does not impact on the proposed guiding principle of protecting the hubs.

The approach by Hastings and Botsford (2006a,b), also provides capacity to describe the persistence of a metapopulation using an integrated approach where the dispersal and population growth formulae are combined. Rather than use a mean field method,

Hastings and Botsford (2006a,b) use an eigenvector approach based on the growth-connectivity matrix. While the conclusions reached, regarding the role of reserves in supporting larval supply, are similar to ours the additional capacity to include more sophisticated graph theoretic measures is limited in the Hastings and Botsford (2006a,b) model. These measures could, for example, include betweenness and closeness values (Estrada and Bodein, 2008) for each population to reflect the metapopulation topology.

Although connectivity is an important criterion in planning reserve networks (Williams et al., 2005), we must keep in mind that connectivity represents a single facet of a metapopulation's dynamics, and the ultimate goal of conservation planning is to ensure metapopulation persistence across the full suite of species. The MPA network which created the highest connectivity in our modelling (LPER (Fig. 1) with an average degree of 98), was not necessarily the most persistent—it was also the interactions between the populations on the protected sites that maximised persistence for that dispersal network (Fig. 1). The selection of a connected suite of sites was described by Cerdeira et al. (2005) but without regard to the complexities of metapopulation dynamics.

To model the interactions of multiple species would require a range of network structures where each reserve site could potentially function differently (i.e. source/sink, stepping stone, etc.). Potentially as the distance of dispersal changes (Botsford et al., 2009) the relevant topological model will also change. Conservation planners will need to integrate the multiple networks to determine the reserve selection priority. Initially selecting key species groups (e.g. broadcast spawning reef fish) that are directly protected by reserve mechanisms may be sufficient for many conservation plans. The mechanisms to combine dispersal networks within a conservation planning framework, such as MARXAN (Ball, 2000; Watts et al., 2009; Bejer et al., 2010), are the focus of ongoing research.

In promoting the consideration of connectivity, we are not advocating that planning for connectivity should take precedence over other conservation principles (Hodgson et al., 2009). It is important to utilise connectivity data in conjunction with other information and not as the only design criteria (Jones et al., 2009; McCook et al., 2009; Bejer et al., 2010). To include connectivity in conservation planning, data on the dispersal behaviour of important organisms must be collected (Botsford et al., 2009). In the absence of connectivity data, conservation planning should proceed by utilising the precautionary principle of treating sites or site groups as independent of each other, in other words, as if no connections existed, and follow standard planning procedures (i.e. comprehensive, adequate, representative) (Stewart et al., 2003) as well as incorporating other objectives such as planning for catastrophes (Allison et al., 2003; Game et al., 2008).

Identification of the relevant connectivity patterns which then influence the associated protection measures is clearly required for designing future MPAs (Mora et al., 2006). This paper creates the theoretical foundations for further exploration of connectivity in the realm of conservation planning.

5. Conclusions

There is an ongoing and widespread debate about principles, efficiency and limitations of selecting sites for MPA networks. Although dispersal connectivity between sites is crucial for the persistence of species that have a pelagic larval phase, connectivity has only had limited impact on real world marine conservation planning (see example for California by Kaplan et al., 2009). Here we present a comprehensive array of dispersal connectivity networks in marine environments, from minimal connectivity up to fully connected complex systems. Our results examine the effects of connectivity patterns on the persistence of metapopulations in MPA

networks that constitute 16% of the total system. As these topological models represent general connectivity patterns, they may be useful when considering the general importance and effects of connectivity to conservation planning in marine systems. We show that when planning for persistence of an MPA network, regardless of which connectivity topological model is considered, sites should be selected to utilise the highly connected regions of the network. This combination of reserve and non-reserve sites will create the larval exchange network with the highest probability of persistence, as well as imparting benefits to the non-reserved parts of the system. However, an important qualifier is that the findings presented here are limited by the metapopulation model (Kininmonth et al., 2010b) and the optimisation heuristic algorithm. In particular the metapopulation model does not include trophic interactions, rescue effects, density dependent selection or demographic influences. The hill climb optimisation heuristic was based on random incremental changes and was not necessarily able to find the optimal solution for reserve placement. Despite these limitations our research shows that identifying the connectivity pattern from our nine topological models and then prioritising the highly connected sites for protection will optimise marine conservation planning efforts.

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References

- Albert, R., Barabasi, A.-L., 2002. Statistical mechanics of complex networks. *Reviews of Modern Physics* 74, 48–94.
- Allison, G.W., Gaines, S.D., Lubchenko, J., Possingham, H.P., 2003. Ensuring persistence of marine reserves: catastrophes require adopting an insurance factor. *Ecological Applications* 13, S8–S24.
- Almany, G.R., Berumen, M.L., Thorrold, S.R., Planes, S., Jones, G.P., 2007. Local replenishment of coral reef fish populations in a marine reserve. *Science* 316, 742–744.
- Almany, G.R., Connolly, S., Heath, D.D., Hogan, J.D., Jones, G.P., McCook, L.J., Mills, M., Pressey, R.L., Williamson, D.H., 2009. Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. *Coral Reefs* 28, 339–351.
- Ball, I.R., 2000. Mathematical applications for conservation ecology: the dynamics of tree hollows and the design of nature reserves, PhD thesis. In: Department of Mathematics. University of Adelaide, Adelaide.
- Barabasi, A.-L., 2009. Scale-free networks: a decade and beyond. *Science* 325, 412.
- Barabasi, A.-L., Albert, R., 1999. Emergence of scaling in random networks. *Science* 286, 509–512.
- Bascompte, J., Possingham, H.P., Roughgarden, J., 2002. Patchy populations in stochastic environments: critical number of patches for persistence. *The American Naturalist* 159, 128–137.
- Beger, M., Simon, L., Game, E.T., Ball, I.R., Treml, E., Watts, M.E., Possingham, H., 2010. Incorporating functional ecological connectivity into spatial decision making for conservation. *Conservation Letters* 4, 359–368.
- Bode, M., Bode, L., Armsworth, P.R., 2006. Larval dispersal reveals regional sources and sinks in the Great Barrier Reef. *Marine Ecology Progress Series* 308, 17–25.
- Bode, M., Burrage, K., Possingham, H.P., 2008. Using complex network metrics to predict the persistence of metapopulations with asymmetric connectivity patterns. *Ecological Modelling* 214, 201–209.
- Botsford, L.W., Hastings, A., Gaines, S.D., 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecology Letters* 4, 144–150.
- Botsford, L.W., Micheli, F., Parma, A.M., 2006. Biological and ecological considerations in the design, implementation and success of MPAs. In: FAO (Ed.), Report of the Expert Workshop on Marine Protected Areas and Fisheries Management: Review of Issues and Considerations. FAO, Rome, pp. 109–148.
- Botsford, L.W., White, J., Coffroth, M.A., Paris, C.B., Planes, S., Shearer, T.L., Thorrold, S.R., Jones, G.P., 2009. Connectivity and resilience of coral reef metapopulations in marine protected areas: matching empirical efforts in predictive needs. *Coral Reefs* 28, 327–337.
- Bridgewater, P.B., 1987. Connectivity: an Australian perspective. In: Saunders, D.A., Arnold, G.W., Burbidge, A.A., Hopkins, A.J.M. (Eds.), *Nature Conservation: The Role of Remnants of Native Vegetation*. Surrey Beatty and Sons Pty, Chipping Norton, pp. 195–200.
- Butts, C., 2009. Revisiting the foundations of network analysis. *Science* 325, 414.
- Byers, J., Pringle, J.M., 2006. Going against the flow: retention, range limits and invasions in advective environments. *Marine Ecology Progress Series* 313, 27–41.
- Cerdeira, J.O., Gaston, K., Pinto, L.S., 2005. Connectivity in priority area selection for conservation. *Environmental Modelling and Assessment* 10, 183–192.
- Crowder, L.B., Lyman, S.J., Figueira, W.F., Priddy, J., 2000. Source-sink population dynamics and the problem of siting marine reserves. *Bulletin of Marine Science* 66, 799–820.
- Csardi, G., Nepusz, T., 2006. The igraph software package for complex network research. *InterJournal, Complex Systems*, 1695, <http://igraph.sf.net>.
- Day, J.R., Fernandes, L., Lewis, A., De'ath, G., Slegers, S., Barnett, B., Kerrigan, B., Breen, D., Innes, J., Oliver, J., Ward, T.J., Lowe, D., 2003. The representative areas programme. In: *Proceedings of the 9th International Coral Reef Symposium*, Bali, Indonesia.
- Dezso, Z., Barabasi, A.-L., 2002. Halting viruses in scale-free networks. *Physical Review E* 65, 055103.
- Drechsler, M., 2009. Predicting metapopulation lifetime from macroscopic network properties. *Mathematical Biosciences* 218, 59–71.
- Erdos, P., Renyi, A., 1959. On random graphs. *Publicationes Mathematicae* 6, 290–297.
- Estrada, E., Bodein, O., 2008. Using network centrality measures to manage landscape connectivity. *Ecological Applications* 18, 1810–1825.
- Fall, A., Fortin, M.-J., Manseau, M., O'Brien, D., 2007. Spatial graphs: principles and applications for habitat connectivity. *Ecosystems* 10, 448–461.
- Fernandes, L., Day, J.R., Kerrigan, B., Breen, D., De'ath, G., Mapstone, B., Coles, R., Done, T., Marsh, H., Poiner, I., Ward, T.M., Williams, D., Kenchington, R., 2009. A process to design a network of marine no-take areas: lessons from the Great Barrier Reef. *Ocean and Coastal Management* 52, 439–447.
- Frank, K., Wissel, C., 2002. A formulae for the mean lifetime of metapopulations in heterogeneous landscapes. *American Naturalist* 159, 530–552.
- Game, E., Watts, M.E., Wooldridge, S., Possingham, H., 2008. Planning for persistence in marine reserves: a question of catastrophic importance. *Ecological Applications* 18, 670–680.
- Graham, E.M., Baird, A.H., Connolly, S., 2008. Survival dynamics of scleratinian coral larvae and implications for dispersal. *Coral Reefs* 27, 529–539.
- Grantham, B.A., Eckert, G.L., Shanks, A.L., 2003. Dispersal potential of marine invertebrates in diverse habitats. *Ecological Applications* 13, S108–S116.
- Hanski, I., 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology* 63, 151–162.
- Hastings, A., Botsford, L.W., 2006a. Persistence of spatial populations depends on returning home. *Proceedings of the National Academy of Sciences of the United States of America* 103, 6067–6072.
- Hastings, A., Botsford, L.W., 2006b. A simple persistence condition for structured populations. *Ecology Letters* 9, 845–852.
- Hodgson, J.A., Thomas, C.D., Wintle, B., Moilanen, A., 2009. Climate change, connectivity and conservation decision making: back to basics. *Journal of Applied Ecology* 46, 964–969.
- Hughes, T., Baird, A.H., Dinsdale, E.A., Moltschanivskiy, N.A., Pratchett, M.S., Tanner, J.E., Willis, B.L., 2000. Supply-side ecology works both ways: the link between benthic adults, fecundity and larval recruits. *Ecology* 81, 2241–2249.
- Jones, G.P., Milicich, M.J., Emslie, M., Lunow, C., 1999. Self-recruitment in a coral reef fish population. *Nature* 402, 802–804.
- Jones, G.P., Planes, S., Thorrold, S.R., 2005. Coral reef fish larvae settle close to home. *Current Biology* 15, 1314–1318.
- Jones, G.P., Russ, G.R., Sale, P.F., Steneck, R., 2009. Theme section on "Larval connectivity, resilience and the future of coral reefs". *Coral Reefs* 28, 303–305.
- Jones, G.P., Srinivasan, M., Almany, G.R., 2007. Population connectivity and conservation of marine biodiversity. *Oceanography* 20, 100–111.
- Kaplan, D., Botsford, M., O'Farrell, L.W., Gaines, M., Jorgensen, S.D.S., 2009. Model-based assessment of persistence in proposed marine protected area designs. *Ecological Applications* 19, 433–448.
- Kininmonth, S., De'ath, G., Possingham, H.P., 2010a. Graph theoretic topology of the Great but small Barrier Reef world. *Theoretical Ecology* 3, 75.
- Kininmonth, S., Drechsler, M., Johst, K., Possingham, H., 2010b. Metapopulation mean life time within complex networks. *Marine Ecology Progress Series* 417, 139–149.
- Kinlan, B.P., Gaines, S.D., 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* 84, 2007–2020.
- Knights, A.M., Crowe, T.P., Burnell, G., 2006. Mechanisms of larval transport: vertical distribution of bivalve larvae varies with tidal conditions. *Marine Ecology Progress Series* 326, 167–174.
- Kraus, G., Pelletier, D., Dubreuil, J., Mollmann, C., Hinrichsen, H.-H., Bastardie, F., Vermard, Y., Mahevas, S., 2008. A model-based evaluation of Marine Protected Areas: the example of eastern Baltic cod (*Gadus morhua callarias* L.). *ICES Journal of Marine Science* 66, 109–121.
- Kritzer, J., Sale, P., 2004. Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. *Fish and Fisheries* 5, 131–140.
- Leicht, E.A., Newman, M.E.J., 2008. Community structure in directed networks. *Physical Review Letters* 100, 118703.
- Leskovec, J., Kleinberg, J., Faloutsos, C., 2007. Graph evolution: densification and shrinking diameters. *ACM Transactions on Knowledge Discovery from Data* 1, 40.

- Lewis, A., 1997. Recruitment and post-recruit immigration affect the local population size of coral reef fishes. *Coral Reefs* 16, 139–149.
- Li, L., Alderson, D., Doyle, J.C., Willinger, W., 2005. Towards a theory of scale-free graphs: definition, properties and implications. *Internet Mathematics* 2, 431–523.
- Mahevas, S., Pelletier, D., 2004. ISIS-Fish, a generic and spatially explicit simulation tool for evaluating the impact of management measures on fisheries dynamics. *Ecological Modelling* 171, 65–84.
- McCook, L.J., Almany, G.R., Berumen, M.L., Day, J.R., Green, A.L., Jones, G.P., Leis, J.M., Planes, S., Russ, G.R., Sale, P.F., Thorrold, S.R., 2009. Management under uncertainty: guide-lines for incorporating connectivity into the protection of coral reefs. *Coral Reefs* 28, 353–366.
- Minor, E., Urban, D., 2008. A graph-theory framework for evaluating landscape connectivity and conservation planning. *Conservation Biology* 22, 297–307.
- Minor, E., Urban, D., 2010. A graph-theory framework for evaluating landscape connectivity and conservation planning. *Conservation Biology* 22, 297–307.
- Moilanen, A., Wilson, K.A., Possingham, H., 2009. *Spatial Conservation Prioritization*. Oxford University Press, London.
- Montoya, J., Sole, R., 2002. Small World patterns in food webs. *Journal of Theoretical Biology* 214, 405–412.
- Mora, C., Andrefouet, S., Costello, M., Kranenburg, C., Rollo, A., Veron, J.E.N., Gaston, K., Myers, R., 2006. Coral reefs and the global network of marine protected areas. *Ecology* 312, 1750–1751.
- Newman, M.E.J., 2006. Modularity and community structure in networks. *Proceedings of the National Academy of Sciences of the United States of America* 103, 8577–8582.
- Pastor-Satorras, R., Vespignani, A., 2002. Epidemic dynamics in finite size scale-free networks. *Physical Review E (R)* 65, 035108.
- Pelletier, D., Mahevas, S., 2005. Spatially explicit fisheries simulation models for policy evaluation. *Fish and Fisheries* 6, 307–349.
- Pitcher, C.R., Doherty, P., Arnold, P., Hooper, J., Gribble, N., Bartlett, C., Browne, M., Campbell, N., Cannard, T., Cappel, M., Carini, G., Chalmers, S., Cheers, S., Chetwynd, D., Colefax, A., Coles, R., Cook, S., Davie, P., De'ath, G., Devereux, D., Done, T., Donovan, T., Ehrke, B., Ellis, N., Ericson, G., Fellegara, I., Forcey, K., Furey, M., Gledhill, D., Good, N., Gordon, S., Haywood, M., Hendriks, P., Jacobsen, I., Johnson, J., Jones, M.S., Kininmonth, S., Kistler, S., Last, P., Leite, A., Marks, S., McLeod, I., Oczkiewicz, S., Robinson, M., Rose, C., Seabright, D., Sheils, J., Sherlock, M., Skelton, P., Smith, D., Smith, G., Speare, P., Stowar, M., Strickland, C., Van der Geest, C., Venables, W., Walsh, C., Wassenberg, T., Welna, A., Yearsley, G., 2007. Seabed Biodiversity on the Continental Shelf of the Great Barrier Reef World Heritage Area. *AIMS/CSIRO/QM/QDPI*, 320 pp.
- Porter, M.A., Onnela, J.-P., Mucha, P.J., 2009. Communities in networks. *Notices of the AMS* 56, 1082–1097.
- Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M., Wilson, K.A., 2007. Conservation planning in a changing world. *Tree* 22, 583–592.
- Roberts, C.M., Reynolds, J.D., Cote, I., Hawkins, J.P., 2006. Redesigning coral reef conservation. In: Cote, I., Reynolds, J. (Eds.), *Coral Reef Conservation*. Cambridge University Press, London.
- Sala, E., Aburto-Oropeza, O., Paredes, G., Parra, I., Barrera, J.C., Dayton, P.K., 2002. A general model for designing networks of marine reserves. *Science* 298, 1991–1993.
- Sale, P., Cowen, R., Danilowicz, B.S., Jones, G.P., Kritzer, J., Lindeman, K., Planes, S., Polunin, N., Russ, G.R., Sadovy, Y., Steneck, R., 2005. Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology and Evolution* 20, 74–80.
- Schumaker, N.H., 1996. Using landscape indices to predict habitat connectivity. *Ecology* 77, 1210–1225.
- Shanks, A.L., Grantham, B.A., Carr, M.H., 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications* 13, 159–169.
- Siegel, D.A., Kinlan, B.P., Gaylord, B., Gaines, S.D., 2003. Lagrangian descriptions of marine larval dispersion. *Marine Ecology Progress Series* 260, 83–96.
- Stewart, R.R., Noyce, T., Possingham, H.P., 2003. Opportunity cost of ad hoc marine reserve design decisions: an example from South Australia. *Marine Ecology Progress Series* 253, 25–38.
- Stewart, R.R., Possingham, H.P., 2003. A framework for systematic marine reserve design in South Australia. *Aquatic Protected Areas—What Works Best and How do We Know? In: Beumer, J.P., Grant, A., Smith, D.C. (Eds.), World Congress on Aquatic Protected Areas Proceedings*, Cairns, Queensland.
- Taylor, P.D., Fahrig, L., Henein, K., Merriam, G., 1993. Connectivity is a vital element of landscape structure. *Oikos* 68, 571–573.
- Treml, E., Halpin, P.N., Urban, D., Pratson, L., 2008. Modelling population connectivity by ocean currents, a graph-theoretic approach for marine conservation. *Landscape Ecology* 23, 19–36.
- Tuck, G.N., Possingham, H.P., 2000. Marine protected areas for spatially structured exploited stocks. *Marine Ecology Progress Series* 192, 89–101.
- Underwood, J.N., Smith, L.D., Van Oppen, M., Gilmour, J., 2007. Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. *Molecular Ecology* 16, 771–784.
- van Oppen, M., Lutz, A., De'ath, G., Peplow, L., Kininmonth, S., 2008. Genetic traces of recent long-distance dispersal in a predominantly self-recruiting coral. *PLoS One* 3, 1–12.
- Visconti, P., Elkin, C., 2009. Using connectivity metrics in conservation planning—when does habitat quality matter? *Diversity and Distributions* 15, 602–612.
- Walters, C.J., Hilborn, R., Parrish, R., 2007. An equilibrium model for predicting the efficacy of the marine protected areas in coastal environments. *Canadian Journal of Fisheries and Aquatic Science* 64, 1009–1018.
- Watts, M.E., Ball, I.R., Stewart, R.R., Klein, C., Wilson, K.A., Steinback, C., Lourival, R., Kircher, L., Possingham, H., 2009. Marxan with zones: software for optimal conservation based land- and sea-use zoning. *Environmental Modelling and Software* 24, 1513–1521.
- Williams, J.C., ReVelle, C.S., Levin, S.A., 2005. Spatial attributes and reserve design models: a review. *Environmental Modelling and Assessment* 10, 163–181.
- Yemane, D., Shin, Y.-J., Field, J.G., 2008. Exploring the effect of Marine Protected Areas on the dynamics of fish communities in the southern Benguela: an individual-based modelling approach. *Journal of Marine Science* 66, 378–387.