



UNIVERSITY OF LEEDS

This is a repository copy of *Strategies in scheduling marine protected area establishment in a network system.*

White Rose Research Online URL for this paper:
<http://eprints.whiterose.ac.uk/141144/>

Version: Published Version

Article:

Kininmonth, S, Weeks, R, Abesamis, RA et al. (5 more authors) (2019) Strategies in scheduling marine protected area establishment in a network system. *Ecological applications* : a publication of the Ecological Society of America, 29 (1). e01820. ISSN 1051-0761

<https://doi.org/10.1002/eap.1820>

© 2018 by the Ecological Society of America. Kininmonth, S, Weeks, R, Abesamis, RA et al. (5 more authors) (2019) Strategies in scheduling marine protected area establishment in a network system. *Ecological applications* : a publication of the Ecological Society of America, 29 (1). e01820. ISSN 1051-0761. <https://doi.org/10.1002/eap.1820>. Reproduced in accordance with the publisher's self-archiving policy.

Reuse

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.



eprints@whiterose.ac.uk
<https://eprints.whiterose.ac.uk/>

Strategies in scheduling marine protected area establishment in a network system

STUART KININMONTH,^{1,2,3,11} REBECCA WEEKS,⁴ RENE A. ABESAMIS,^{4,5} LAWRENCE PATRICK C. BERNARDO,⁶
MARIA BEGER,^{7,8} ERIC A. TREML,^{9,10} DAVID WILLIAMSON,⁴ AND ROBERT L. PRESSEY⁴

¹Stockholm Resilience Centre, Stockholm University, Kräftriket, Sweden

²Centre for Ecological and Evolutionary Synthesis, University of Oslo, Oslo, Norway

³School of Marine Studies, The University of South Pacific, Suva, Fiji

⁴ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland, Australia

⁵Silliman University-Angelo King Center for Research and Environmental Management, Dumaguete City, Philippines

⁶Nadaoka Laboratory, Department of Civil Engineering, Tokyo Institute of Technology, Tokyo, Japan

⁷University of Queensland, Brisbane, Queensland, Australia

⁸School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, UK

⁹University of Melbourne, Melbourne, Victoria, Australia

¹⁰School of Life and Environmental Sciences, Deakin University, Geelong, Victoria, Australia

Citation: S. Kininmonth, R. Weeks, R. Abesamis, L. P. C. Bernardo, M. Beger, E. A. Treml, D. Williamson, and R. L. Pressey. 2019. Strategies in scheduling marine protected area establishment in a network system. *Ecological Applications* 29(1):e01820. 10.1002/eap.1820

Abstract. Instantaneous implementation of systematic conservation plans at regional scales is rare. More typically, planned actions are applied incrementally over periods of years or decades. During protracted implementation, the character of the connected ecological system will change as a function of external anthropogenic pressures, local metapopulation processes, and environmental fluctuations. For heavily exploited systems, habitat quality will deteriorate as the plan is implemented, potentially influencing the schedule of protected area implementation necessary to achieve conservation objectives. Understanding the best strategy to adopt for applying management within a connected environment is desirable, especially given limited conservation resources. Here, we model the sequential application of no-take marine protected areas (MPAs) in the central Philippines within a metapopulation framework, using a range of network-based decision rules. The model was based on selecting 33 sites for protection from 101 possible sites over a 35-yr period. The graph-theoretic network criteria to select sites for protection included PageRank, maximum degree, closeness centrality, betweenness centrality, minimum degree, random, and historical events. We also included a dynamic strategy called colonization–extinction rate that was updated every year based on the changing capacity of each site to produce and absorb larvae. Each rule was evaluated in the context of achieving the maximum metapopulation mean lifetime at the conclusion of the implementation phase. MPAs were designated through the alteration of the extinction risk parameter. The highest ranked criteria were PageRank while the actual implementation from historical records ranked lowest. Our results indicate that protecting the sites ranked highest with regard to larval supply is likely to yield the highest benefit for fish abundance and fish metapopulation persistence. Model results highlighted the benefits of including network processes in conservation planning.

Key words: conservation planning; larval networks; marine protected areas; metapopulation; PageRank algorithm; Philippines; scheduled implementation.

INTRODUCTION

Instantaneous implementation of systematic conservation plans at regional scales is rare. Though examples do exist, these have been in idiosyncratic contexts (Fernandes et al. 2005). More typically, planned actions are applied over periods of years or decades (Pressey et al. 2013). Meanwhile, anthropogenic pressures and environmental

fluctuations will be ongoing, decreasing the conservation value of unprotected areas (Visconti et al. 2010), and changing the character of the connected ecological system. For heavily exploited systems, habitat quality will deteriorate as the plan is being implemented (Fig. 1), potentially compromising planners' ability to achieve conservation objectives.

Within this context, and given limited resources available for conservation, understanding the best strategy to adopt for scheduling protected area designation is desirable (Margules and Pressey 2000, Pressey and Taffs 2001, Strange et al. 2006, Stewart et al. 2007). Scheduling calls for the formulation and solution of a dynamic area

Manuscript received 5 February 2018; revised 27 May 2018; accepted 20 August 2018; final version received 7 October 2018.
Corresponding Editor: Éva E. Plaganyi.

¹¹ E-mail: Stuartjk@ibv.uio.no

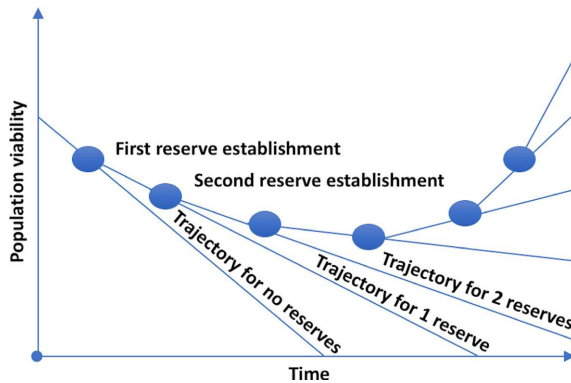


FIG. 1. Conceptual model of progressive implementation of reserves in a declining system. The trajectory for no reserves continues to decline without intervention to a minimal level of population persistence. If a reserve is added at a later time then the trajectory is altered but may still be negative. As subsequent reserves are added, the trajectories for the population change their rate of decline. Eventually, with sufficient reserves established, the trajectory of the population persistence becomes positive and is thus less susceptible to the pressure of over exploitation.

selection problem in which protection and loss are incremental and proceed in parallel (Costello and Polasky 2004). This is not straightforward for conservation objectives aimed at representing biodiversity features, and is further complicated when dynamic biodiversity processes that underpin feature persistence are considered (Visconti et al. 2010, Brown et al. 2015).

Most marine species have a pelagic larval phase during which larvae may disperse orders of magnitude further than they move as adults (Almany et al. 2009, Weersing and Toonen 2009, Treml et al. 2012, Puckett et al. 2014, Green et al. 2015). A direct consequence of this larval dispersal is that small, isolated, marine protected areas (MPAs) will be insufficient to ensure the persistence of marine metapopulations (Botsford et al. 2001, Mora et al. 2006). Ensuring population persistence, especially where species are directly exploited by fisheries, will require networks of MPAs that are connected through larval exchange (Botsford et al. 2001, Begger et al. 2010, 2015, Worboys et al. 2015, Olds et al. 2016) and with suitable habitat quality (Cabral et al. 2016). Moreover, the effectiveness of each MPA, and hence the network as a whole, depends upon the spatial relationships between protected sites (Magris et al. 2016). This presents clear implications for scheduling where MPA networks are implemented over a period of time during which extractive activities and associated loss of habitat values are ongoing.

Decision rules that enhance the dispersal of fish larvae have been proposed as a basis for quantifying aspects of habitat connectivity and for prioritizing sites for inclusion in MPA networks (Treml et al. 2008, Begger et al. 2010, 2015, Jacobi and Jonsson 2011, Kininmonth et al. 2011, White et al. 2014). For example, strategies to select

sites for conservation could include the PageRank algorithm (Allesina and Pascual 2009), maximum degree, minimal degree, closeness, or betweenness centrality (Jacobi and Jonsson 2011, Andrello et al. 2014, Magris et al. 2014). The efficacy of network-based decision rules in informing conservation scheduling strategies has yet to be explored however.

Here, we compare the effectiveness of different strategies for scheduling the sequential designation of MPAs within a connected environment. We compare strategies based on different network-based decision rules with the actual implementation of MPAs over a 35-yr period in a case study region in the central Philippines. Connectivity between MPAs was defined by a modeled larval dispersal network. The ability of MPA networks created following different scheduling strategies to promote population persistence was assessed using a relative measure of metapopulation mean life time (MLT; Kininmonth et al. 2010).

METHODS

Case study region

We selected a study region in the central Philippines where no-take MPAs have been established through time since 1974 (Figs. 2, 3; Appendix S1 Alcala et al. 2008). The first successful no-take MPA in the Philippines (Apo Island Reserve, established in 1982), situated within this region, served as a template for MPA legislation and co-management nationwide (Alcala and Russ 2006). As such, the history of MPA establishment within the region can be considered as a good case study for the expansion of local marine management in the Philippines and perhaps the wider Coral Triangle region.

We divided the fringing coral reefs in the study region into 101 sites of equal dimensions (4.8-km² grid cells, Fig. 2). Small (0.02–0.76 km²) MPAs were established in 33 of these sites between 1974 and 2008 while 68 sites remained fully open to fishing (Appendix S1).

Reserve modeling within a metapopulation framework

The evaluation of MPA network ability to promote population persistence requires a measure of change in the ecological dynamics of the region. A significant influence for fish dynamics is the transfer of larvae from one reef site to another. Hence, we evaluated the best strategy for scheduling the allocation of MPAs for the Philippines case study region using a metapopulation approach based on a larval dispersal model. Graph theory was used to formulate the migration in the metapopulation while population persistence was measured by the MLT developed by Kininmonth et al. (2010). Nine different network measures (Table 1) were used to select the sequential set of reserves and then the MLT was recorded at each time step. Strategies with the highest MLT were considered to be superior.



Fig. 2. Map of Philippines study area and location of potential marine protected areas. Sites containing coral reef habitat are numbered 1–101. Each site containing reef habitat has a history of protection or currently remains fully open to fishing and a candidate for future protection.

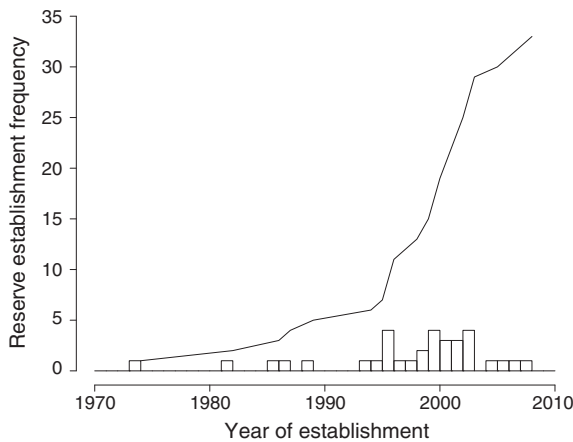


Fig. 3. History of designation of marine protected areas in central Philippines. Bars show annual numbers of marine protected areas established. Line shows cumulative number.

Larval dispersal network

We defined a larval transport network for the study region by modeling the dispersal and successful settlement of fish larvae among the 101 sites. Hydrodynamic forcing of the dispersal model was driven by best-available data on regional sea surface currents over three years (2006–2008) provided by a two-dimensional global ocean model (U.S. Navy Layered Ocean Model). A major driver of probable larval dispersal patterns in the

study region is the Bohol Jet current that is present throughout the year (Gordon et al. 2011, Abesamis et al. 2016). This strong westward current exhibits significant seasonal variability but is relatively stable from year to year including extreme opposite anomalous years (El Niño and La Niña; Hurlburt et al. 2011). Key larval characteristics were roughly based on coral reef snappers (Lutjanidae). Virtual larvae in the model had a pelagic larval duration (PLD) of 30 d (Paris et al. 2005). Larval swimming speed was set to 0.15 m/s, which is at the lower end of swimming speeds of settlement-stage larval snappers measured in the field (Leis 2006). Three thousand virtual larvae were released from each site for two months per year (June and September), staggered over several days. Larvae had randomized starting positions clustered around the center of each site with a spread of about 40% of the site length. Dispersal of early-stage larvae (first half of PLD) was governed by Euler-type advection–diffusion equations adapted from Polovina et al. (1999). Swimming and orientation capabilities in late-stage larvae (second half of PLD) were incorporated by adding a swimming velocity term to the advection velocity components and directing swimming toward the nearest site found within a radius of 4.4 km (equivalent to the width of two grid cells in the model) from each larva’s position. No larval mortality rate was implemented. Larval transport probabilities in the resulting matrix were expressed as the magnitude of settlement to a receiver site normalized by the total number of larvae released from a source site (scaled by the

TABLE 1. Scheduling strategies for marine protected areas evaluated for persistence of populations due to larval connectivity.

Strategy for scheduling MPAs	Description
(1) Actual implementation	Sites are described by both their reserve status and the year of establishment.
(2) Maximum degree	Sites ranked from highest to lowest based on the degree (k_i) or number of all connections present in the larval transport network.
(3) Minimum degree	Sites ranked from lowest to highest based on the degree (k_i) or number of all connections present in the larval transport network.
(4) Closeness centrality	Sites ranked according to the mean length of the shortest average minimum path length (L) from the site to all other sites. This measure captures how close the site is to the central region of the network.
(5) Betweenness centrality	Sites ranked according to how often the shortest average minimum path length (L) passes through the site. This measure captures the “stepping stone” capacity of the site required to link other parts of the network efficiently.
(6) PageRank	Counting the number and local density of both in and out links ranks the sites. The local density in this model relates to the degree distribution of the neighboring sites. The index measures how well connected the site is to the entire network given the local neighborhood configuration.
(7) Colonization–extinction rate	Sites ranked by their colonization–extinction rate that is updated every year based on the changing capacity of each site to produce and absorb larvae. This measure captures the flow of larvae both in and out of the potential reserve based on linkage strength and number of connections.
(8) Random	Sites ranked randomly.
(9) No MPAs selected	Sites not ranked since none are selected for reserve nomination.

source site’s reef area). Our approach in modeling larval dispersal was to capture the general pattern of probable larval transport among the 101 sites, which is likely to be largely defined by regional hydrodynamics, rather than to parameterize the model to reflect more specific ecological traits or events (e.g., formation of spawning aggregation sites). The resulting larval transport incidence matrix also implies that connectivity patterns are constant from year to year. In reality, however, connectivity patterns may vary between years depending on factors such as the timing of reproduction (Carson et al. 2010, Watson et al. 2011, Treml et al. 2012). Nonetheless, variations in probable connectivity patterns suggested by our larval dispersal model are unlikely to have a large impact on evaluating the relative effectiveness of the different scheduling strategies.

Network model

We incorporated larval connectivity into a 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 (Treml et al. 2008, Kininmonth et al. 2009). 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 neighboring 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 $\mathfrak{A}_i (i \in V_1, \dots, V_n)$ within the set of neighbors for a selected vertex divided by the maximum possible neighbor 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 $L_{\text{Min}}(i, j)$ 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 pair of vertices in a network. Each vertex i has the attribute for reef 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 . Models were analysed using the igraph package in R (Csardi and Nepusz 2006).

Based on the larval transport incidence matrix, we generated a graph containing 101 vertices (reef sites). The weight of each edge was derived from the larval transport probabilities, creating a fully connected network (Fig. 4).

Metapopulation persistence model

Following Drechsler (2009) local populations have an 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 more environmental variability and consequently a relatively larger extinction rate. As described in Kininmonth et al. (2011:Eq. 2), the summation of the outbound edge weights (w_{ij}) for each vertex (referred to as vertex strength s_i^{out}) was used to measure the emigration rate

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

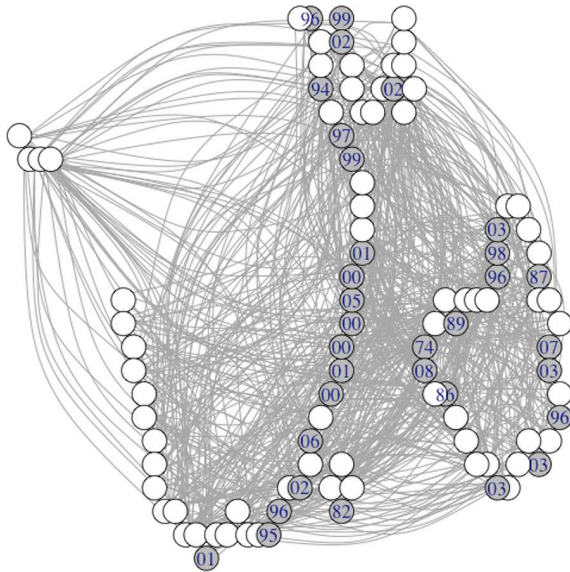


FIG. 4. The network of larval transport with links less than 0.005 removed. Actual reserves are shown in gray with labels indicating the year (last two digits of the year) of implementation. The nodes are positioned relative to their latitude and longitude.

The rate at which a site i was colonized was based on the number of successful recruits needed to restart a colony (μ), inbound edge weights (w_{ji}), and the extinction rate of each neighbor in the local neighborhood (v_j ; Kininmonth et al. 2011)

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

The colonization strength of each site (Eq. 4) is essentially a measure of the dispersal capacity from the neighboring sites

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

We calculated the colonization–extinction ratio for each site using the harmonic mean of Eqs. 3 and 4 (Drechsler 2009; Eq. 8)

$$U_i = \left(\frac{1}{2} (u_i^{\text{in}})^{-2} + \frac{1}{2} (u_i^{\text{out}})^{-2} \right)^{-1/2}. \quad (5)$$

The aggregated geometric mean of the colonization–extinction ratio (Drechsler 2009; Eq. 9) for the entire network q (Eq. 6) was then combined with the geometric mean of the local extinction rates v (Eq. 7)

$$q = \prod_{i=1}^N \left\{ \max(U_i, \sqrt{2}) \right\}^{1/N} \quad (6)$$

$$v = \prod_{i=1}^N v_i^{1/N} \quad (7)$$

to calculate the approximate MLT of the entire metapopulation (consisting of N populations) in the study area (Drechsler 2009; Eq. 11)

$$\text{MLT} = \frac{1}{v} \sum_{i=1}^N \sum_{k=1}^N \frac{1}{k} \frac{(N-i)!}{(N-k)!} \frac{1}{(N-1)^{k-i}} \varepsilon^{k-i}. \quad (8)$$

We set the species-specific coefficient ε to 45, following exploration of the parameter space and reference to numerical estimation in Hanski (1999), Drechsler et al. (2003), and Nicholson et al. (2006). We chose a rather small value of $\eta = 0.2$ for each site, which represents strong environmental stochasticity (Drechsler 2009). This increased variability of the environmental pressures on the population results in increased extinction rates. Therefore, as the value of η increases the extinction rate decreases. The area of each site was nominally set at 5 ha (roughly equivalent to the modal size of MPAs in the study region), and the value of the minimum number of immigrants required (u) was set at 2.

Strategies for scheduling MPA designation

We modeled the sequential implementation of MPAs under nine different scheduling strategies (Table 1). For comparison with the actual sequence of establishment of existing MPAs, we began all sequences assuming there were no MPAs established at the beginning of each scheduling strategy. In addition to the actual schedule of MPA implementation (Fig. 4), we compared the efficacy of five scheduling strategies informed by static network metrics, and a dynamic strategy based on the colonization–extinction ratio of each site. While not exhaustive, these strategies have particular emphasis on utilizing information that can be derived from understanding the structure of the larval dispersal network. The strategy selection attempted to capture the primary measures of larval dispersal. Two baseline strategies, one in which MPAs were selected at random, and one in which no MPAs were selected, were included for comparison.

Maximum degree, minimum degree, closeness centrality, betweenness centrality, and PageRank metrics were derived from the larval dispersal network (Table 1). To utilize local network metrics such as maximum and minimum degree, we removed the weaker edges with probability values of less than 0.005. The colonization–extinction ratio for each site was calculated using the method of Kininmonth et al. (2010).

For each scheduling strategy, we first ranked all sites based on the nominated strategy (Table 1). At each time step, sites were selected for MPA implementation in rank order, with the number of sites determined by the actual

implementation schedule (Fig. 3). In the situation where a site’s rank was tied with another, the site with the lowest ID number (Fig. 2) was selected. We modeled the impact of MPA designation by increasing the value of η from 0.2 to 10 to reflect a reduction in environmental pressure. Following each MPA designation, we calculated the MLT value for the entire network. This process was repeated for 34 iterations, directly reflecting the expansion of the actual MPA system from 1974 to 2008 to a total of 34 MPAs (Fig. 3). For the random strategy, we repeated this process 10 times to capture the variability in MLT outputs.

RESULTS

The nine scheduling strategies based on the single larval dispersal network (Fig. 4), containing 101 nodes and 675 edges, generated MLT values from 11.2 to 3,313.2 yr at the 35th year of the schedule (Table 2). The ranking of the strategies across the 35 yr remained essentially consistent (Fig. 5). The strategies can be ranked as follows; PageRank, betweenness centrality, colonization–extinction rate, maximum degree, random, closeness centrality, minimum degree, actual implementation, and none. The random strategy generated values from 10 iterations of 2,065–2,084 ($2,072.7 \pm 10.3$ [mean \pm SD]) and thus ranked above closeness centrality. The actual implementation schedule generated an MLT of 1,776.1 and thus was ranked lowest of the strategies that

TABLE 2. Mean lifetime (MLT) values at the final 35th year for each strategy based on the Philippines’ case study larval dispersal network, ordered from the highest MLT to lowest.

Strategy	MLT at final year	Ranking
PageRank	3,313.2	1
Betweenness	3,280.1	2
Colonization–extinction rate	2,954.9	3
Maximum degree	2,876.7	4
Random	2,072.7 mean, 10.3 SD	5
Closeness	2,056.7	6
Minimum degree	2,050.6	7
Actual implementation	1,776.1	8
No reserves designated	11.2	9

implemented MPAs (and above “none”), just after minimum degree. Notably, closeness centrality, minimum degree, and actual implementation were below the range of values achieved by random allocation. It should be noted that the ideal strategy of simultaneous implementation of all reserves in the first year was not evaluated, since this does not reflect the reality of MPA scheduling in the region. Rankings did not alter when the edges were randomly rewired or when a scalar value was applied to the edge weights implying that the algorithm selection is robust against these variations in network configuration.

The MLT values did not generate a smooth curve across the 35 yr (Fig. 5). Instead, there was little

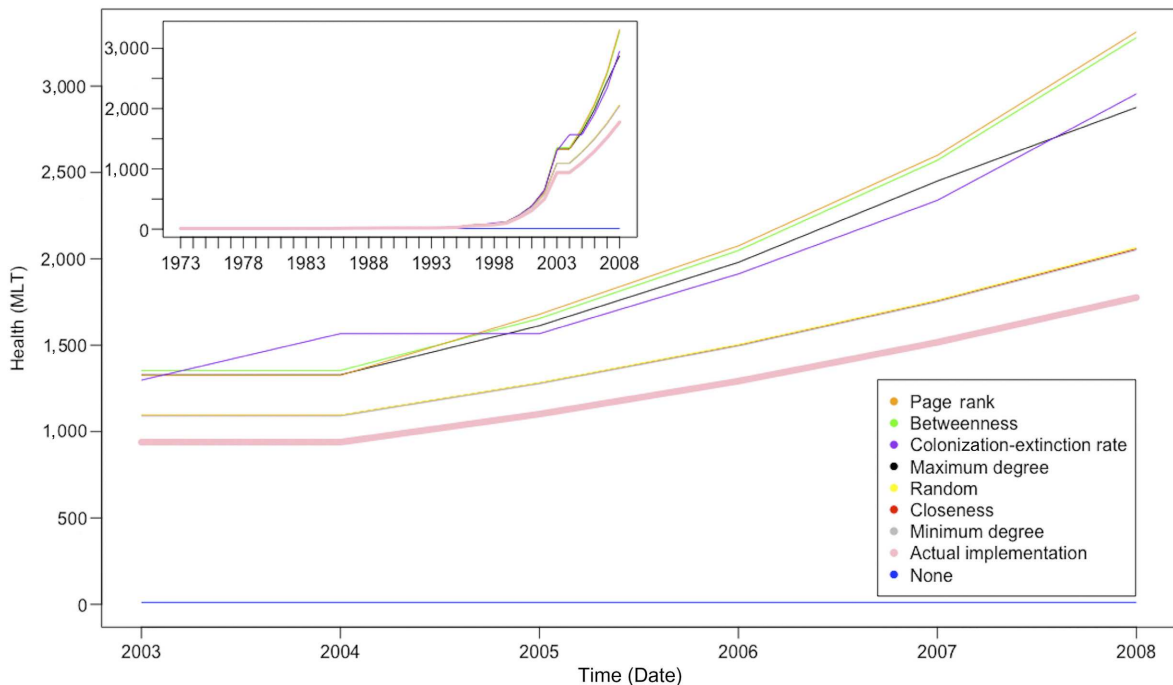


FIG. 5. Graph of metapopulation mean lifetime (MLT) values for each yearly time step (insert shows all years) for each scheduling strategy. The final ranked order is listed sequentially in the legend, noting that some indices (such as closeness and minimum degree) are overlapping with others (see Table 2).

increase in the MLT for any of the strategies until year 23, after which the MLT increased at higher rates. This non-linear change in MLT was a direct result of the variation in implementation rate (see cumulative line in Fig. 3). Changing the homogeneous extinction rates (0.1–2.0) or the areas of sites (0.05–0.10 km²) did not alter the rank order of strategies. The ranking did not change when the schedule was altered to be uniformly distributed across the years.

DISCUSSION

The best strategy for achieving metapopulation persistence in this case study was to schedule sites for new designation as MPAs based on the PageRank index (186% increase in MLT from the actual implementation). This index essentially valued sites that were strongly connected to the entire network through the density and strength distributions of the local neighborhood (see Allesina and Pascual 2009). Other strategies, including the actual schedule of MPA implementation, were less able to generate the same metapopulation MLT. The MLT values are useful only in a comparative sense within a ranking scheme and thus quantitative assessments of the strategies are of limited value.

Surprisingly, the random allocation of MPAs also outperformed the actual implementation schedule. This indicates that the metapopulation MLT algorithm is sensitive to the density of connections within the network. In general, the random selection process will distribute MPAs evenly throughout the network, thus capturing

some areas of the seascape not included in the existing MPA network. This contrasts with the actual implementation schedule that showed evidence of missing protection within the densely connected region (center in Fig. 6A, Fig. 4, Sites 22–40 in Fig. 2). The impact of network density on the larval supply across the entire network is that sites with high larval export are enhanced by MPA designation and are more likely to act as even stronger larval sources to other MPAs. This additional feedback mechanism is important within this MLT algorithm. Hence, the PageRank strategy (Fig. 6B) of enhancing high-density regions first with MPAs that have maximum contact with unprotected sites is in agreement of the findings based on optimal selection of sites for no-take protection by Kininmonth et al. (2011) and Andrello et al. (2014).

Unexpectedly the dynamic index based on the evolving measure of colonization–extinction rate ranked only third, after PageRank and betweenness centrality. The dynamic index is updated with every time step (yearly in this case study) based on the capacity of the larval supply dynamics to influence the persistence of the local and entire metapopulation. The colonization–extinction ratio schedule forces each new MPA addition to enhance the colonization capacity of the local neighborhood thereby contributing to the persistence of the entire metapopulation. The higher success of the PageRank and betweenness measures, over stochastic metapopulation dynamics, implies that each site can be ranked simply on the local neighborhood structure in the first year of the schedule. Capturing those sites that form key larval sources while

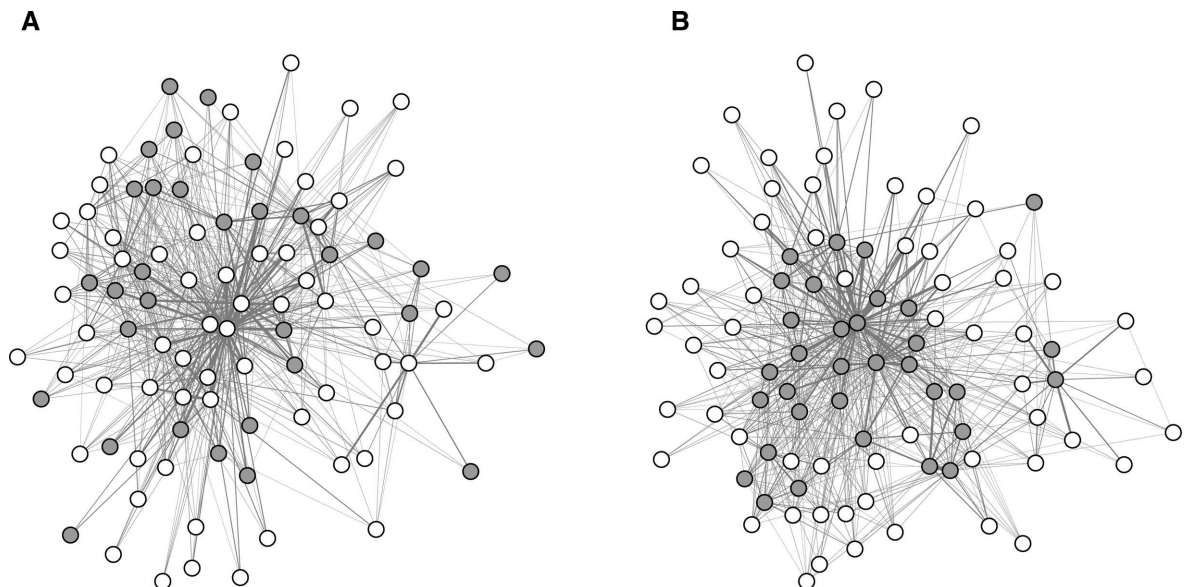


FIG. 6. The graph of larval dispersal for (A) the actual implementation schedule and (B) the PageRank algorithm showing the distribution of 33 “gray” reserves relative to the overall network (similar to Fig. 4). The central sections of each network contain a higher density of connections. The edge thickness is proportional to the modeled larval transfer numbers. The graph is drawn using a Fruchterman Reingold algorithm (Csardi and Nepusz 2006), which attempts to position the nodes in two dimensions with edges being as equal as possible and the minimum number of crossings.

connected to the high-density unprotected sites appears to be the basis for the best strategy in MPA selection, especially over an extended period. This implementation strategy does rely on the topology of the network having regions of higher density than others, as observed in other marine systems (Kininmonth et al. 2009, Watson et al. 2011, Treml et al. 2015). Rules such as even spacing of reserves across the network (McCook et al. 2009) fail to accommodate the dynamics across the network, but may be required to offset catastrophic events (Game et al. 2008). The more clustered a network is (i.e., the existence of highly connected regions separated by areas of sparse connections), the more successful PageRank and betweenness centrality approaches to scheduling will be. Shifting reserves around to match the dynamics of the hydrodynamics and fish behavior are not practical, and we have adopted a long-term approach to the region's spatial planning exercise.

While our comparison of scheduling strategies includes an actual implementation case in the Philippines, the use of single metrics such as larval flow in hydrodynamic networks is not recommended as the sole basis for MPA selection (Fernandes et al. 2005, Cabral et al. 2016, Weeks et al. 2016). The results here simply indicate the impact of including network measures into the entire process, which will also require gaining social confidence and enforcement capacity of local communities. The MLT metapopulation model presented here is also simplified through the use of a static larval dispersal network, uniform reef areas, and homogeneous probability of site disturbance. Social benefits such as the support of conservation opportunity (Alcala and Russ 2006, Knight and Cowling 2007) by stakeholders, in this case local fishing communities, may outweigh the negativities of allocating funds for MPA establishment to sites with lower rankings for PageRank or betweenness. Applying a more holistic approach to MPA network design (Fernandes et al. 2005, 2009, Brown et al. 2015) will include the larval supply ranking as only one component and, as such, the final prioritization ranking is likely to differ from the network-based ranking.

Our ranking of site priorities is a static function of the frequency of MPA allocation since the larval contribution of each site is assumed to reflect only the reserve status and position in the larval supply network. There is typically a significant lag period for the transition of an exploited or unprotected site to a high-capacity MPA (Abesamis et al. 2014, Edgar et al. 2014) and this lag period was not included in the modeling formulation here. The modeling conducted here assumes the MPAs are fully restored immediately and so, unless the area of the MPA is altered, the ranking will remain stable. Coupling the adult populations to the larval supply is principally through the attention to habitat quality (Cabral et al. 2016). In our model, the habitat was treated as uniform in the absence of data for all sites. However, considerable variation in habitat quality in the modeled system is likely (Abesamis et al. 2016) and would almost

certainly influence the extinction rate of the populations within the context of this model.

While the estimation of the colonization aspects involved in the modeling of larval supply was based on sophisticated biophysical modeling, the extinction risk was considered homogeneous. This is unlikely to be the case given the complex geography of the region. A more sophisticated extinction risk model could be developed based on historical records of cyclone damage and surveys of fish and their habitats, perhaps even with climate change effects (Álvarez - Romero et al. 2018). The algorithm in this model would tend to favor the protection of sites with lower risk of extinction and hence allocate MPAs to stable regions first.

The extent of the case study was selected to encompass the scale of dispersal and to incorporate a region undergoing change in marine management. However, there is not an absolute boundary for larval dispersal and outside influences could have an impact on the metapopulation model used here. There does not appear to be an easy solution to this problem. The larval transport model could be expanded, but this would still have latent effects across the metapopulation and be difficult to parameterize, especially in such intricate island complexes.

Protracted implementation is particularly common where the region is wholly or partly under private ownership or other arrangements that finely subdivide management (Pressey and Taffs 2001), as in inshore waters of the Philippines. Given how common this situation is, not nearly enough attention is paid to scheduling, especially with spatial prioritization (Magris et al. 2014). The concept of marine degradation being "rescued" by protection measures (Fig. 1), such as reserves, highlight that the regional metapopulation viability may be at risk unless a critical level of reserves is enabled. Exactly what this threshold is, and how dynamic it is, will be determined by a repeated cycle of monitoring and reserve management. Hence, the methods proposed here are designed to highlight the integration of dynamic processes across the region into conservation planning.

CONCLUSION

The explicit use of larval dispersal networks to inform the scheduling of reserve implementation highlights three key design considerations. First, the selection of sites should be biased toward those that are strongly connected to the network as measured by an index such as PageRank. Second, the sites should be distributed to capture all high-density components of the network rather than concentrated in one or two sectors. Third, the reserves with the highest ranking for larval connectivity, measured by PageRank for example, should be established first. We demonstrated here that utilizing the connections between sites can be included as a component in the process of MPA selection across an extended time period to maximize the persistence of species in an MPA network. This

comparison extends the centrality network metrics that can be included in planning software such as MARXAN (Watts et al. 2009) but importantly the modeling presented here does not replace the use of these planning tools.

ACKNOWLEDGMENTS

The workshop that gave rise to this paper was funded by R. L. Pressey through the ARC Centre of Excellence for Coral Reef Studies. R. Weeks, M. Beger, and R. L. Pressey acknowledge the Australian Research Council for funding support. ARC funding to Garry Russ and Angel Alcalá supported larval dispersal modeling. Cesar Villanoy helped develop the larval dispersal model. S. Kininmonth acknowledges that this research was funded through the 2015-2016 BiodivERsA COFUND call for research proposals, with the national funders FORMAS. We also thank the detailed and thoughtful comments from two reviewers.

LITERATURE CITED

- Abesamis, R. A., A. L. Green, G. R. Russ, and C. R. L. Jadloc. 2014. The intrinsic vulnerability to fishing of coral reef fishes and their differential recovery in fishery closures. *Reviews in Fish Biology and Fisheries* 24:1033–1063.
- Abesamis, R. A., B. L. Stockwell, L. P. C. Bernardo, C. L. Villanoy, and G. R. Russ. 2016. Predicting reef fish connectivity from biogeographic patterns and larval dispersal modelling to inform the development of marine reserve networks. *Ecological Indicators* 66:534–544.
- Alcalá, A. C., and G. R. Russ. 2006. No-take marine reserves and reef fisheries management in the Philippines: a new people power revolution. *Ambio* 35:245–254.
- Alcalá, A. C., A. A. Bucol, and P. Nillos-kleiven. 2008. Directory of marine reserves in the Visayas. SUAKCREM and Foundation for the Philippine Environment, Dumaguete City, Philippines.
- Allesina, S., and M. Pascual. 2009. Googling food webs: Can an eigenvector measure species' importance for coextinctions? *PLoS Computational Biology* 5:e1000494.
- Almany, G. R., S. R. Connolly, D. D. Heath, J. D. Hogan, G. P. Jones, L. J. McCook, M. Mills, R. L. Pressey, and D. H. Williamson. 2009. Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. *Coral Reefs* 28:339–351.
- Álvarez - Romero, J. G., et al. 2018. Designing connected marine reserves in the face of global warming. *Global Change Biology* 24:e671–e691. <https://doi.org/10.1111/gcb.13989>
- Andrello, M., M. N. Jacobi, S. Manel, W. Thuiller, and D. Mouillot. 2014. Extending networks of protected areas to optimize connectivity and population growth rate. *Ecography* 38:273–282.
- Beger, M., L. Simon, E. Game, I. Ball, E. Treml, M. Watts, and H. P. Possingham. 2010. Incorporating functional ecological connectivity into spatial decision making for conservation. *Conservation Letters* 3:359–368.
- Beger, M., J. McGowan, E. A. Treml, A. L. Green, A. T. White, N. H. Wolff, C. J. Klein, P. J. Mumby, and H. P. Possingham. 2015. Integrating regional conservation priorities for multiple objectives into national policy. *Nature Communications* 6:8208.
- Botsford, L. W., A. Hastings, and S. D. Gaines. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecology Letters* 4:144–150.
- Brown, C. J., C. White, M. Beger, H. S. Grantham, B. S. Halpern, C. J. Klein, V. J. D. Mumby Tulloch, M. Ruckelshaus, and H. P. Possingham. 2015. Fisheries and biodiversity benefits of using static versus dynamic models for designing marine reserve networks. *Ecosphere* 6:182.
- Cabral, R. B., S. D. Gaines, M. T. Lim, M. P. Atrigenio, S. S. Mamauag, G. C. Pedemonte, and P. M. Aliño. 2016. Siting marine protected areas based on habitat quality and extent provides the greatest benefit to spatially structured metapopulations. *Ecosphere* 7:e01533.
- Carson, H. S., P. C. López-Duarte, L. Rasmussen, D. Wang, and L. A. Levin. 2010. Reproductive timing alters population connectivity in marine metapopulations. *Current Biology* 20:1926–1931.
- Costello, C., and S. Polasky. 2004. Dynamic reserve site selection. *Resource and Energy Economics* 26:157–174.
- Csardi, G., and T. Nepusz. 2006. The igraph software package for complex network research. *InterJournal, Complex Systems* 1695:1–9.
- Drechsler, M. 2009. Predicting metapopulation lifetime from macroscopic network properties. *Mathematical biosciences* 218:59–71.
- Drechsler, M., K. Frank, I. Hanski, R. B. O'Hara, and C. Wisel. 2003. Ranking metapopulation extinction risk: from patterns in data to conservation management decisions. *Ecological Applications* 13:990.
- Edgar, G., et al. 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506:216–220.
- Fernandes, L., et al. 2005. Establishing representative no-take areas in the great barrier reef: Large-scale implementation of theory on marine protected areas. *Conservation Biology* 19:1733–1744.
- Fernandes, L., et al. 2009. A process to design a network of marine no-take areas: Lessons from the Great Barrier Reef. *Ocean & Coastal Management* 52:439–447.
- Game, E. T., E. McDonald-Madden, M. L. Puotinen, and H. P. Possingham. 2008. Should we protect the strong or the weak? Risk, resilience, and the selection of marine protected areas. *Conservation Biology: the Journal of the Society for Conservation Biology* 22:1619–1629.
- Gordon, A. L., J. Sprintall, and A. Ffield. 2011. Regional oceanography of the Philippine Archipelago. *Oceanography* 24:14–27.
- Green, A. L., A. P. Maypa, G. R. Almany, K. L. Rhodes, R. Weeks, R. A. Abesamis, M. G. Gleason, P. J. Mumby, and A. T. White. 2015. Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews* 90:1215–1247.
- Hanski, Metapopulation. 1999. Ecology. Oxford University Press, New York, New York, USA.
- Hurlburt, H. E., E. J. Metzger, J. Sprintall, S. N. Riedlinger, R. A. Arnone, T. Shinoda, and X. Xu. 2011. Circulation in the Philippine Archipelago simulated by 1/12° and 1/25° Global HYCOM and EAS NCOM. *Oceanography* 24:28–47. <https://doi.org/10.5670/oceanog.2011.02>
- Jacobi, M. N., and P. R. Jonsson. 2011. Optimal networks of nature reserves can be found through eigenvalue perturbation theory of the connectivity matrix. *Ecological Applications* 21:1861–1870.
- Kininmonth, S. J., G. Death, and H. P. Possingham. 2009. Graph theoretic topology of the Great but small Barrier Reef world. *Theoretical Ecology* 3:75–88.
- Kininmonth, S., M. Drechsler, K. Johst, and H. Possingham. 2010. Metapopulation mean life time within complex networks. *Marine Ecology Progress Series* 417:139–149.

- Kininmonth, S., M. Beger, M. Bode, E. Peterson, V. M. Adams, D. Dorfman, D. R. Brumbaugh, and H. P. Possingham. 2011. Dispersal connectivity and reserve selection for marine conservation. *Ecological Modelling* 222:1272–1282.
- Knight, A. T., and R. M. Cowling. 2007. Embracing opportunism in the selection of priority conservation areas. *Conservation Biology* 21:1124–1126.
- Leis, J. M. 2006. Are larvae of demersal fishes plankton or nekton? *Advances in Marine Biology* 51:59–141.
- Magris, R. A., R. L. Pressey, R. Weeks, and N. C. Ban. 2014. Integrating connectivity and climate change into marine conservation planning. *Biological Conservation* 170:207–221.
- Magris, R. A., E. A. Treml, R. L. Pressey, and R. Weeks. 2016. Integrating multiple species connectivity and habitat quality into conservation planning for coral reefs. *Ecography* 39:649–664.
- Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. *Nature* 405:243–253.
- McCook, L. J., et al. 2009. Management under uncertainty: guide-lines for incorporating connectivity into the protection of coral reefs. *Coral Reefs* 28:353–366.
- Montoya, J. M., and R. V. Sole. 2002. Small world patterns in food webs. *Journal of Theoretical Biology* 214:405–412.
- Mora, C., S. Andréfouët, M. J. Costello, C. Kranenburg, A. Rollo, J. Veron, K. J. Gaston, and R. A. Myers. 2006. Enhanced: coral reefs and the global network of marine protected areas. *Science* 312:1750–1751.
- Nicholson, E., M. I. Westphal, K. Frank, W. A. Rochester, R. L. Pressey, D. B. Lindenmayer, and H. P. Possingham. 2006. A new method for conservation planning for the persistence of multiple species. *Ecology Letters* 9:1049.
- Olds, A. D., et al. 2016. Quantifying the conservation value of seascape connectivity: a global synthesis. *Global Ecology and Biogeography* 25:3–15.
- Paris, C. B., R. K. Cowen, R. Claro, and K. C. Lindeman. 2005. Larval transport pathways from Cuban snapper (*Lutjanidae*) spawning aggregations based on biophysical modeling. *Marine Ecology Progress Series* 296:93–106.
- Polovina, J. J., P. Kleiber, and D. R. Kobayashi. 1999. Application of TOPEX-POSEIDON satellite altimetry to simulate transport dynamics of larvae of spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands 1993–1996. *Fishery Bulletin* 97:132–143.
- Pressey, R. L., and K. H. Taffs. 2001. Scheduling conservation action in production landscapes: priority areas in western New South Wales. *Biological Conservation* 100:355–376.
- Pressey, R. L., M. Mills, R. Weeks, and J. C. Day. 2013. The plan of the day: Managing the dynamic transition from regional conservation designs to local conservation action. *Biological Conservation* 166:155–165.
- Puckett, B. J., D. B. Eggleston, P. C. Kerr, and R. A. Luettich. 2014. Larval dispersal and population connectivity among a network of marine reserves. *Fisheries Oceanography* 23:342–361.
- Stewart, R. R., I. R. Ball, and H. P. Possingham. 2007. The effect of incremental reserve design and changing reservation goals on the long-term efficiency of reserve systems. *Conservation Biology* 21:346–354.
- Strange, N., B. J. Thorsen, and J. Bladt. 2006. Optimal reserve selection in a dynamic world. *Biological Conservation* 131:33–41.
- Treml, E. A., P. N. Halpin, D. L. Urban, and L. F. Pratson. 2008. Modeling population connectivity by ocean currents, a graph-theoretic approach for marine conservation. *Landscape Ecology* 23:19–36.
- Treml, E. A., J. Roberts, Y. Chao, P. Halpin, H. P. Possingham, and C. Riginos. 2012. Reproductive output and duration of the pelagic larval stage determine seascape-wide connectivity of marine populations. *Integrative and Comparative Biology* 52:525–537.
- Treml, E. A., J. Roberts, P. N. Halpin, H. P. Possingham, and C. Riginos. 2015. The emergent geography of biophysical dispersal barriers across the Indo-West Pacific. *Diversity and Distributions* 21:465–476.
- Visconti, P., R. L. Pressey, D. B. Segan, and B. A. Wintle. 2010. Conservation planning with dynamic threats: the role of spatial design and priority setting for species' persistence. *Biological Conservation* 143:756–767.
- Watson, J. R., D. A. Siegel, B. E. Kendall, S. Mitarai, A. Rassweiler, and S. D. Gaines. 2011. PNAS Plus: Identifying critical regions in small-world marine metapopulations. *Proceedings of the National Academy of Sciences USA* 108: E907–E913.
- Watts, M. E., I. R. Ball, R. S. Stewart, C. J. Klein, K. Wilson, C. Steinback, R. Lourival, L. Kircher, and H. P. Possingham. 2009. Marxan with zones: software for optimal conservation based land- and sea-use zoning. *Environmental Modelling & Software* 24:1513–1521.
- Weeks, R., A. L. Green, E. Joseph, N. Peterson, and E. Terk. 2016. Using reef fish movement to inform marine reserve design. *Journal of Applied Ecology* 54:145–152.
- Weersing, K., and R. J. Toonen. 2009. Population genetics, larval dispersal, and connectivity in marine systems. *Marine Ecology Progress Series* 393:1–12.
- White, Wilson J., Julianna Schroeger, Patrick T. Drake, and Christopher A. Edwards. 2014. The value of larval connectivity information in the static optimization of marine reserve design. *Conservation Letters* 7:533–544.
- Worboys, E. G. L., R. Ament, J. C. Day, H. Locke, G. Tabor, and S. Woodley. 2015. Consultation draft, guidelines for connectivity conservation: part one, definition: connectivity conservation area. Gland, Switzerland.

SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1820/full>

DATA AVAILABILITY

Data are available from Mendeley Data: <https://doi.org/10.17632/mcgywvn6cz.1>