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Incorporating larval dispersal into MPA design for both conservation and fisheries

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Running Head

Incorporating dispersal into MPA design

Abstract

Larval dispersal by ocean currents is a critical component of systematic marine protected area (MPA) design. However, there is a lack of quantitative methods to incorporate larval dispersal in support of increasingly diverse management objectives, including local population persistence under multiple types of threats (primarily focused on larval retention within and dispersal between protected locations) and benefits to unprotected populations and fisheries (primarily focused on larval export from protected locations to fishing grounds). Here, we present a flexible MPA design approach that can reconcile multiple such potentially conflicting management objectives by balancing various associated treatments of larval dispersal information. We demonstrate our approach based on alternative dispersal patterns, combinations of threats to populations, management objectives, and two different optimization strategies (site vs. network-based). Our outcomes highlight a consistently high efficiency in selecting priority locations that are self-replenishing, inter-connected, and/or important larval sources. We find that the opportunity to balance these three dispersal attributes flexibly can help not only to prevent meta-population collapse, but also to ensure effective fisheries recovery, with average increases in the number of recruits at fishing grounds at least two-times higher than achieved by standard habitat-based or ad-hoc MPA designs. Future applications of our MPA design approach should therefore be encouraged, specifically where management tools other than MPAs are not feasible.

Key words

Connectivity, ocean currents, conservation, fisheries management, marine protected areas, MPAs, marine reserves, network, Marxan

Introduction

Most benthic marine animals have a planktonic life history period during which their eggs and larvae drift in the ocean for days, weeks or even months until they settle back to benthic habitats. Settlement habitats range from being close to home (Jones et al. 2005) to being 10s-

100s of kilometres away from spawning locations (Shanks et al. 2003, Shanks 2009, Jones 2015). The complete process from spawning and dispersal to settlement is a key component of population connectivity (for review see Cowen and Sponaugle 2009), and it represents a potentially critical driver of the demography and evolution of coastal marine species (Roughgarden et al. 1988, Doherty and Fowler 1994, Palumbi 1994, Hellberg 1996, Carson et al. 2011). While demographic and evolutionary implications of connectivity through larval dispersal (hereafter called connectivity) are uncertain (Marshall et al. 2010), it is clear that any given pool of settling larvae constitutes the basis of the future replenishment and genetic makeup of resident populations. Owing to this direct link to population dynamics, connectivity is functionally analogous to the isolation of patches in classic meta-population theory (Hanski 1998) and a key factor to consider in the design of marine protected areas (MPAs) (Gaines et al. 2003, Gaines et al. 2010).

MPAs are coastal and marine environments that are regulated, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values (sensu Dudley 2008). We distinguish this broad definition of MPAs here from that of marine reserves or no-take zones, in which strictly no fishing is allowed (e.g. Green et al. 2014). By our definition, an MPA can be equivalent to a marine reserve, but it can also comprise a network of multiple marine reserves and other management zones with variable levels of fishery restrictions. Importantly, the placement or spatial design of protected areas can help optimize dynamic interactions between population recovery, larval production and connectivity. However, systematic MPA designs based on larval dispersal information are complicated by (1) the long-standing challenge to track larvae directly in the field (Sale et al. 2005) and (2) a paucity of quantitative methods that can utilize dispersal data in order to achieve particular management outcomes.

Over recent years, seminal progress has been made in measuring larval dispersal based on chemical tags and genetic parentage analysis (Jones et al. 2009, Jones 2015), and in simulating it based on biophysical models (Cowen and Sponaugle 2009, Kool et al. 2013). Oceanographic and modelling data in particular are now widely available. In many cases, estimates of larval transport by ocean currents appear to be correlated with measured population genetic variation (Galindo et al. 2006, Kool et al. 2010, White et al. 2010, Kool et al. 2011, Crandall et al. 2012, Foster et al. 2012, Crandall et al. 2014), confirming the potential utility of simulated connectivity for systematic MPA design. Direct measurements of larval dispersal are still rare, but first results appear to be consistent with common management objectives, including self-recruitment in individual reserves (Almany et al. 2007), larval export from reserves to fished areas (Harrison et al. 2012), and connectivity across reserve networks (Planes et al. 2009). While alignments of field observations with biophysical models are still rare (e.g. Sponaugle et al. 2012), simulating dispersal patterns provides the only feasible option to project connectivity for multiple species across entire seascapes (Treml et al. 2015) and advance associated MPA design theory.

The first methods allowing incorporation of connectivity into MPA design were qualitative and generic, emphasizing, for example, that priority locations for the placement of marine reserves should be self-replenishing and net sources of larvae to fished sites (see Roberts et al. 2003a). The first quantitative methods relied on indirect connectivity metrics, such as the level of clustering of reserves within a network (Possingham et al. 2000, Leslie et al. 2003), or simple nearest-neighbour measurements of connectivity that likely fail to capture underlying meta-population dynamics (Moilanen and Hanski 2001). Actual connectivity information has firstly been incorporated into MPA design based on estimates of the scale of larval dispersal distances (Sala et al. 2002). Dispersal distances are still the primary connectivity data available and frequently used to establish ecological guidelines or “rules of thumb” for MPA design (Green et al. 2015), which help field practitioners make more informed decisions on the size and spacing of protected areas required to ensure efficient protection of resident populations (Green et al. 2014, Green et al. 2015). However, ecological guidelines are generic and tend to be applied manually rather than by using systematic MPA design software, such as Marxan and Zonation, which would allow users to optimize connectivity outcomes explicitly (Ball et al. 2009, Lehtomäki and Moilanen 2013).

For example, several recent studies have highlighted the use of network metrics, such as eigenvalue centrality, degree centrality, betweenness centrality or mean meta-population lifetime, to identify candidate sites with the greatest presumed importance for marine meta-population persistence (Bode et al. 2008, Jacobi and Jonsson 2011, Kininmonth et al. 2011, Watson et al. 2011, White et al. 2014, Magris et al. 2015). A more intuitive alternative, which might also be less prone to sacrificing critical connectivity information (Moilanen 2011), is to optimize larval dispersal directly; for example, by penalizing strong export of larvae from protected to unprotected locations (Beger et al. 2010), or by setting species-specific targets for local larval retention within reserves (White et al. 2014). Larval dispersal can also be optimized very strategically in order to design MPAs that are likely to facilitate particular ecological outcomes, such as species persistence under climate change (Mumby et al. 2011).

All of these recent studies present important advances in systematic MPA design, but flexible quantitative approaches with the capacity to integrate increasingly diverse management goals for biodiversity conservation and fisheries management are still lacking (Jones et al. 2007, Green et al. 2014). This is an important shortcoming, because the priorities for global MPA implementation following the Convention on Biological Diversity in 1992 and the World Summit on Sustainable Development in 2002 have shifted from biodiversity conservation to wider ecosystem services, primarily including fisheries (e.g. White and Green 2014). Current MPA design approaches do not match this development, likely because the treatment of larval dispersal data for conservation benefits (primarily focused on retaining larvae within protected area boundaries) (Botsford et al. 2001) is in fundamental contrast to fisheries management objectives (primarily focused on the export of larvae from reserves to fishing grounds) (Hastings and Botsford 2003). Here, we present a transparent and flexible MPA design approach to reconcile multiple such potentially conflicting management outcomes by integrating three important dispersal attributes: (1) local larval retention (self-replenishment at protected locations), (2) import-connectivity (the magnitude and diversity of external larval subsidies at protected locations), and (3) export-connectivity (the magnitude and diversity of larval subsidies from protected locations to unprotected locations). We use multiple realistic dispersal patterns, types of threats to populations, management objectives, and optimization strategies (site-based vs. network-based) to demonstrate a consistently high performance of our MPA design approach. The outcomes encourage future applications, specifically where natural resource management tools other than MPAs are not feasible.

Methods

We developed our MPA design approach by firstly specifying desirable connectivity characteristics for alternative management objectives, including (1) priority locations to protect for biodiversity conservation, because they ensure the persistence of resident populations by retaining and/or importing larvae from multiple other locations; (2) priority locations to protect in order to support fisheries, because they replenish important fished locations with larvae, and (3) priority locations to be subjected to fishing pressure, because they import many larvae from multiple other locations (Table 1). We then used these simple rules to formulate two connectivity optimization strategies, which we will refer to in the following as "site-characteristics" and "network" strategy. Both strategies use one algorithm to influence population trends within protected area boundaries, which is the focus of basic biodiversity conservation, and another to influence population trends outside of protected area boundaries, which is the focus for wider biodiversity conservation as well as fisheries management (Fig. 1). The two algorithms are then combined into a single connectivity objective function.

Site-characteristics optimization strategy

Algorithms for our first dispersal optimization strategy were formulated to match standard practice in MPA planning, which is to use static maps of desirable features, such as the amount of different habitats, to find the highest overall sum of conservation or management value of individual locations relative to the effectiveness (usually costs) of protecting these locations. Such an optimization strategy based on local features assumes that the functioning of any specific protected location is unaffected by the constellation of other protected locations around it, thereby ignoring potential network effects. However, connectivity optimization based on local dispersal characteristics is (1) easy to integrate with popular MPA design software, such as Marxan (Ball et al. 2009), and (2) computationally less demanding than network-based dispersal optimization.

To support populations in protected locations, our site-characteristics strategy sums up connectivity scores for individual locations to calculate metric P_S (equation 1).

$$P_S = \sum_{i=1}^{m} x_i\big((1 - w_{\mathrm{I}})\mathrm{R}(L_{i,i}) + w_{\mathrm{I}}\mathrm{I}(\hat{L}_{\mathrm{I},i}, z_{\mathrm{I}}, D_{\mathrm{I},j})\big), w_{\mathrm{I}} \in [0, 1], \tag{1}$$

where m is the number of locations and x_i is the status of location i as either protected ($x_i = 1$) or fished ($x_i = 0$). R is a function of local larval retention $L_{i,i}$, which we define here as the number of native settlers relative to local larval output, because this metric is more appropriate to assess population persistence than self-recruitment (the proportion of native settlers relative to the total number of settlers) (see Botsford et al. 2009, Burgess et al. 2014) or absolute numbers of larvae retained in populations of poorly studied demography. I is a function of the sum of larval import from source destinations j into location i ($\hat{L}_{\mathrm{I},i}$), the scaling parameter z_I, and the desirability score $D_{\mathrm{I},j}$: $\mathrm{I}(\hat{L}_{\mathrm{I},i}, z_\mathrm{I}, D_{\mathrm{I},j}) = \sum_{\substack{j=1 \\ j\neq i}}^{m} L_{j,i}^{z_\mathrm{I}} D_{\mathrm{I},j}$, where z_I allows users to adjust whether connection strength or diversity is optimized (Opsahl et al. 2010), and where $D_{\mathrm{I},j}$ can be used to rank the importance of each individual import connection. Most intuitively, the scaling parameter z_I can be used to optimize either connection strengths (numbers of exchanged larvae), which is achieved by setting $z_\mathrm{I} = 1$, or connection diversity (numbers of larval sources), which is achieved by setting $z_\mathrm{I} \approx 0$. Setting z_I exactly to 0 will assign connectivity values of 1 to all pairs of locations (even those that do not exchange larvae) so this parameterization should not be used. Intermediate values for z_I (e.g. 0.5) should be chosen with care, given that the down-weighting of connection strengths will be non-linear (Appendix S1: Fig. S1). Finally, w_I is the import weighting factor, which balances whether larval transport into protected locations is considered less important ($w_\mathrm{I} < 0.5$), equally important ($w_\mathrm{I} = 0.5$) or more important ($w_\mathrm{I} > 0.5$) to support protected populations than local larval retention. Low relative importance of larval import can be assumed if dominant threats are localized, predictable and manageable through reserves, such as fishing pressure. If there are additional threats, which might be global, less easily predictable and non-manageable through reserves, such as climate change or cyclones, then larval import from other locations could be important to support protected populations against unforeseen disturbance. In the latter case, specifying the desirability of specific import connections ($D_{\mathrm{I},j}$) can help ensure that larval sources themselves are least likely to suffer from disturbance; for example, by excluding highly threatened sources j from the optimization ($D_{\mathrm{I},j} = 0$).

To support populations outside of protected area boundaries, we formulated a connectivity metric U_S that specified larval export from protected to unprotected locations (equation 2).

$$U_S = \sum_{i=1}^{m} x_i \mathrm{E}(\hat{L}_{\mathrm{E},i}, z_\mathrm{E}, D_{\mathrm{E},j}), \tag{2}$$

where $\mathrm{E}\left(\hat{L}_{\mathrm{E},i}, z_\mathrm{E}, D_{\mathrm{E},j}\right) = \sum_{\substack{j=1 \\ j\neq i}}^{m} L_{i,j}^{z_\mathrm{E}} D_{\mathrm{E},j}$. Similar to I above, this equation calculates the sum of larval export from a location i to destinations j ($\hat{L}_{\mathrm{E},i}$), allowing users to adjust both the weighting of connection strength relative to connection diversity (z_E) as well as the desirability of each export destination j ($D_{\mathrm{E},j}$). Here, we define $D_{\mathrm{E},j}$ based on relative fishing effort, noting that various other definitions of desirability would be equally feasible. For example, practitioners might aim to mitigate climate change impacts by siting reserves and prioritizing larval export connections to other areas based on measurements of thermal stress (Mumby et al. 2011). The scaling parameter z_E fulfilled the same role as described above for larval import. That is, setting $z_\mathrm{E} = 1$ will maximize numbers of exported larvae, while setting $z_\mathrm{E} < 1$ will down-weight connection strengths in favour of the number of export destinations (Fig. 1 and S1).

Network optimization strategy

Our network optimization strategy was based on the same assumptions about desirable dispersal attributes as the site-characteristics strategy, but metrics P and U were calculated based on the performance of an entire network of protected locations rather than on the sum of values of individual protected locations. In other words, the network strategy directly acknowledges that the performance of individual protected locations within a network depends upon the location of all other protected locations within that network. Capturing this dependency of meta-population dynamics on the status of all subpopulations can be important, but it is also more computationally demanding.

To support protected populations, our network optimization strategy maximized metric P_N as formulated in equation 3.

$$P_N = (1 - w_\mathrm{I}) \sum_{i=1}^{m} x_i \mathrm{R}(L_{i,i}) + w_\mathrm{I} \sum_{i=1}^{m} \sum_{\substack{j=1 \\ j \neq i}}^{m} x_i x_j \, \mathrm{I}(L_{j,i}^{z_\mathrm{I}}, D_{\mathrm{I},j}), w_\mathrm{I} \in [0,1]. \tag{3}$$

The first summand in this equation calculates self-replenishment at location i, expressed again as local larval retention, and considered only if i is currently protected ($x_i = 1$). The second summand calculates larval import among protected locations, because connectivity will only be considered whenever both connected locations are currently protected ($x_i = x_j = 1$). As above, import connectivity is only considered if the weighting factor w_I is greater than 0, while exponent z_I modifies whether connectivity represents numbers of larvae ($z_\mathrm{I} = 1$) or numbers of connections ($z_\mathrm{I} \approx 0$). Also as above, individual import connections can be ranked by multiplication with $D_{\mathrm{I},j}$.

To support unprotected populations, metric U_N was formulated as shown in equation 4.

$$U_N = \sum_{i=1}^{m} \sum_{\substack{j=1 \\ j \neq i}}^{m} x_i (1 - x_j) \, \mathrm{E}(L_{i,j}^{z_\mathrm{E}}, D_{\mathrm{E},j}). \tag{4}$$

Here, E is a function again of $L_{i,j}^{z_\mathrm{E}}$ and $D_{\mathrm{E},j}$, which are multiplied to subsidize the most highly fished export destinations j with maximum larval supply from protected locations ($z_\mathrm{E} = 1$), or to facilitate long-term persistence at highly fished export destinations by maximizing the diversity of protected larval sources ($z_\mathrm{E} \approx 0$). Note that, in contrast to equation 2, larval export to a destination j is taken into account only if j is currently unprotected ($x_j = 0$). However, the most important difference between equations 3 and 4 (P_N and U_N) and between equations 1 and 2 above (P_S and U_S) is that the summation over j is part of the optimization, assessing the value of an entire network of protected locations during every optimization step.

Regardless of which optimization strategy is used, metrics P and U can then be combined to calculate an overall connectivity metric C (equation 5).

$$C = (1 - w_\mathrm{E})P + w_\mathrm{E}U, \; w_\mathrm{E} \in [0, 1], \tag{5}$$

where w_E (an equivalent to w_I) is the export weighting factor, which allows users to balance the treatment of larval dispersal in favour of populations in protected ($w_\mathrm{E} < 0.5$) or unprotected ($w_\mathrm{E} > 0.5$) locations. The maximum value of C across a wide range of possible MPA designs can be used to identify the optimal set of locations to protect.

We note that the magnitude of R, I and E is highly variable, which means that proportional weighting of all three of these dispersal metrics according to w_I and w_E can be achieved only by normalization. For the site-characteristics optimization strategy, this was done here by using percentages of maxima across i. For the network strategy, we used conversion factors based on means across i, i.e. mean R relative to mean I (for w_I) and mean R + I weighted by w_I relative to E (for w_E).

Optimization procedure

The connectivity optimization equations above can be combined with other primary MPA design objectives. The most common of such objectives is to minimize the economic costs for meeting an overarching conservation goal, such as habitat protection (equation 6).

$$H = \sum_{i=1}^{m} c_i x_i, \quad \text{subject to} \quad \sum_{i=1}^{m} a_{i,k} x_i \geq t_k \; \forall \; k. \tag{6}$$

Here, H is our habitat protection metric, c_i is the cost of protecting location i, and $a_{i,k}$ is the area or proportion of conservation features k at that location (e.g. different habitat types), which we aim to increase until associated targets t_k have been achieved. This formulation of H represents the standard type of MPA optimization (Possingham et al. 2000, Ball et al. 2009). Connectivity metric C can be integrated with H in order to calculate a new overall MPA performance metric T for any given spatial design (equation 7).

$$T = H - CSM\ C \tag{7}$$

where CSM is the connectivity strength modifier, which adjusts the overall importance of connectivity in the optimization problem (Watts et al. 2009, Beger et al. 2010). MPA designs can then be optimized by using simulated annealing with subsequent iterative improvement to minimize T, such as implemented in Marxan (Ball et al. 2009). Here, we used 10^4-10^6 iterations in 100 repeat runs for each optimization problem.

We highlight that integrating two (or more) objective functions as in equation 7 can be complicated by the appropriate calibration of the *CSM*. For example, practitioners might aim to combine habitat representation and connectivity objectives. Similar to the calibration of the boundary length modifier in standard Marxan applications (Game and Grantham 2008), a potentially wide range of *CSM* values must then be analysed in order to characterize any potential trade-offs to achieve both management objectives. We use a case study (the Sunda Banda seascape) as an example to describe such a calibration procedure in more detail below.

Idealized connectivity scenarios

The first set of MPA design scenarios aimed to test our new optimization approach under variable management conditions and patterns of larval dispersal. We started this analysis by accessing a realistic connectivity dataset available from dispersal simulations of coral trout (*Plectropomus leopardus*) larvae across 425 coral reef areas in the south-east Asian “Coral Triangle” region (Beger et al. 2015). Three out of approximately 400 subsets of 50 neighbouring coral reef areas extracted from this original dataset were chosen to represent variable dispersal characteristics. We will refer to these local subsets of data in the following as “advective”, “patchy”, and “hotspots” dispersal patterns (Fig. 2). The “advective” dispersal pattern was identified based on the maximum observed sum of differences between upstream and downstream connectivity among reef areas. The “patchy” pattern was identified based on the maximum observed number of completely isolated reef areas (no connections to surrounding reefs). The “hotspots” pattern was identified based on the maximum observed standard deviation in connectivity among reef areas.

We then created three management scenarios, all of which aimed at maximizing MPA performance while achieving an overarching 10% target for the protection of coral reef areas, which are equivalent here to individual subpopulations within a meta-population. The first two scenarios assumed a collapsing meta-population, which was subject to heavy local stress through fishing, but which was unaffected by threats that local protection could not help control (e.g. global climate change). Both scenarios assumed that, in the absence of any protection, fishery harvest depleted total recruitment across all subpopulations by 90% compared to unfished conditions. Where protection was enforced, subpopulations and thus local larval production was assumed to recover to unfished levels. In fished areas, in contrast, larval production was assumed to decline further, because total fishing effort across the entire meta-population was constant. That is, fishing pressure in unprotected areas was directly proportional to protected area coverage (Halpern et al. 2004). Subject to these assumptions, the first idealized management scenario (“maximum retention”) aimed to select the optimal 10% of locations to protect in no-take reserves to ensure maximum local retention, and thus subpopulation persistence. In contrast, the second management scenario (“export to fishing grounds”) aimed to subsidize fisheries productivity by balancing local larval retention and the export of larvae to the most important fishing grounds.

Under the third management scenario, we assumed that our subpopulations were subject not only to locally manageable but also to non-manageable (global) threats. Without any protection, total recruitment into the meta-population was assumed again to be depleted by 90%, but all subpopulations retained the capacity to recover in full once they were protected.

However, recovery success was not guaranteed due, for example, to unforeseen coral bleaching or cyclone disturbance, which we mimicked by inducing the complete collapse of half of all subpopulations. While the selection of subpopulations to collapse was done at random, we ensured that they represented 50% of both protected and unprotected subpopulations. The management aim in this third scenario ("meta-population persistence") was to prevent the collapse of the entire meta-population by balancing local larval retention within and maximum larval supply between reserves.

To achieve the management aims outlined above, we parameterized the first scenario (maximum local retention in reserves under manageable threats) by setting both the import and export weighting parameters to 0. For the second scenario (fishery benefits under manageable local threats), we set the export weighting parameter to 0.5 and the export scaling parameter to 1, placing equal priority on local retention in reserves and on sending as many larvae as possible from reserves to heavily fished areas. For the third scenario (meta-population persistence under manageable and non-manageable threats), we set the import weighting parameter to 0.5 and the import scaling parameter to 1, balancing local retention in reserves and the inter-replenishment between reserves (see Fig. 1).

Alongside our two connectivity optimization strategies, we also used a habitat-representation and a random design strategy in order to assess MPA design performance. The objective of the habitat-representation strategy was to simply maximize the amount of protected coral reef area, while the random strategy used an ad-hoc selection of sites without any underlying rationale.

To contrast MPA performance for each of these optimization strategies, we used a dynamic model. The model was based on an annual time step and run until equilibrium conditions between fishery harvest and recruitment were achieved (25 years). For simplicity, the model assumed a meta-population that was recruitment-dependent, experiencing 100% mortality prior to the next recruitment pulse in each year. Each year of a simulation was started with a spawning event, larval dispersal, and the subsequent arrival of settlers (S) in all subpopulations: $\boldsymbol{S} = \boldsymbol{P} \times \boldsymbol{L}$, where $\boldsymbol{P}$ is a two-dimensional matrix of dispersal probabilities among all subpopulations specific to each connectivity scenario (Fig. 2), and $\boldsymbol{L}$ is a one-dimensional vector of local larval output (or egg production). Given that $\boldsymbol{S}$ is not necessarily representative of successful establishment in adult populations (i.e. recruitment), we then used Beverton and Holt's (1957) recruitment compensation function to incorporate post-settlement density-dependent mortality of larvae (equation 8).

$$R_i = \frac{S_i}{\alpha + \beta S_i}, \text{with } \alpha = \frac{1-h}{4h}, \text{and } \beta = \frac{5h-1}{4hS_{0,i}}, \tag{8}$$

where R_i is recruitment at location i calculated according to the number of settlers at that location, and the initial slope and asymptote of the recruitment compensation curve specified by constants α and β. $S_{0,i}$ is larval settlement under unfished conditions, which we calculated for any given $\boldsymbol{P}$ as the total sum of larvae arriving at locations i when larval output from all locations reflected local coral reef areas, as in dispersal simulations (Beger et al. 2015). The compensation or steepness parameter h can be modified to represent populations that are more (low steepness: small h) or less (high steepness: large h) vulnerable to larval supply. The opposite effect is evident in terms of fisheries productivity, which will deviate relatively strongly (high steepness) or weakly (low steepness) from the exploitable maximum for a given change in larval supply (Appendix S1: Fig. S2). In order to avoid double-counting mortality processes already accounted for in explicit dispersal simulations, we corrected recruitment calculations according to equation 8 by multiplying α by the dominant eigenvalue of $\boldsymbol{P}$ (White 2010).

For a wide range of empirical estimates of h (0.3-0.95) (Myers et al. 1999), we then used our model to calculate the proportion of unfished recruitment in reserves ("maximum retention" scenario), the proportion of recruitment in fished areas relative to recruitment under optimum fishery conditions ("export to fishing grounds" scenario), and the proportion of unfished meta-population recruitment ("meta-population persistence" scenario). Unfished recruitment at each location ($R_{0,\mathrm{i}}$) was calculated by substituting S_i in equation 8 for $S_{0,i}$. The product of $R_i/R_{0,\mathrm{i}}$ and $S_{0,i}$ was used to calculate unfished larval output $L_{0,i}$. Thus, $L_{0,i}$ was the value for larval output assigned also to any currently protected location i (x_i = 1) that did not experience non-manageable disturbance (only relevant for the "meta-population persistence" scenario). Unfished meta-population recruitment (R_0) was calculated as the sum of $R_{0,\mathrm{i}}$ across all i. Recruitment under optimum fishery conditions was calculated as recruitment providing for maximum excess recruitment (MER). For this, we firstly determined the proportion of unfished larval settlement providing for MER (S_{MER}/S_0) (equation 9).

$$\frac{S_{\mathrm{MER}}}{S_0} = \frac{\sqrt{\frac{4h}{1-h}-1}}{\frac{4h}{1-h}-1}, \tag{9}$$

We note that this ratio is equivalent to the proportion of unfished fish biomass delivering the maximum sustainable yield (B_{MSY}) in classic fishery models (Mangel et al. 2013). Via simulation, we confirmed that S_{MER}/S_0 was unaffected by prior corrections of α. We then substituted S_i in equation 8 for $S_{\mathrm{MER},i}$ to calculate $R_{\mathrm{MER},i}$. Optimum meta-population recruitment (R_{MER}) was calculated as the sum of $R_{\mathrm{MER},i}$ across i.

Fishery harvest in each subpopulation was assumed to reflect an unrestricted "ideal free distribution" (IFD), which implies that fishers have perfect knowledge of meta-population dynamics and optimal exploitation. The IFD was implemented by assigning a relative fishing effort and catch per subpopulation that was directly proportional to local numbers of recruits. In consequence, the Catch Per Unit of Effort (CPUE) was spatially uniform. The sum of recruits available to fishers under optimum fishery conditions in an open system was used as a reference against which fishery performance under various MPA design scenarios was contrasted. We note that small-scale fisheries on coral reefs will not always be able to distribute effort freely, but that the IFD is a common and suitable reference model, specifically for comparative purposes (Abernethy et al. 2007).

Sunda Banda case study

Following these idealized scenarios, we then designed a network of MPAs for a region in south-eastern Indonesia whose currently existing network of MPAs is under consideration for modification and extension. The region is known as the Sunda Banda seascape, covering >1 million km^2 from the Lesser Sunda islands in the South, to Sulawesi in the North, and the entire province of Maluku next to Papua New Guinea in the East. Located in the heart of the "Coral Triangle", which is the world's centre of marine biodiversity and conservation priority (Veron et al. 2011), the Sunda Banda seascape harbours exceptionally diverse marine ecosystems, which are increasingly threatened by both local (e.g. fishing and pollution) and global (e.g. rising water temperatures) anthropogenic stressors (see Wang et al. 2015). In line with regional conservation priorities, we selected coral reef protection throughout the Sunda Banda as an applied example of MPA network design with a requirement to meet both a minimum habitat representation target as well as optimum connectivity from the perspective of biodiversity conservation and fisheries. Fisheries are a critical source of food and income in Indonesia, but coral reefs in particular are often heavily overfished (Geronimo and Cabral 2013). Therefore, the Indonesian government has repeatedly expressed its strong desire to increase fisheries production, which is to be achieved partly by designing MPAs that can help sustain or rebuild otherwise largely unregulated fishing grounds.

We started our Sunda Banda case study by generating a coral reef modelling environment consisting of 10 × 10 km grid cells. The amount of coral reef area in each grid cell was assigned based on spatial habitat data freely available from the Lesser Sunda Banda Seascape Atlas (LSBSA, sbsatlas.reefbase.org). We then simulated larval dispersal by using a biophysical model and methods detailed in several previous studies (Treml et al. 2012, Treml et al. 2015). Altogether five spawning profiles for different groups of species, all of which are primary targets of coral reef fisheries in the Sunda Banda region, were used to specify biological parameters of our dispersal model (see Appendix S1: Table S1). Global HYCOM ocean current data (Chassignet et al. 2007) were used to calculate the physical transport of larvae. The final products from dispersal simulations were 100 two-dimensional matrices of dispersal probabilities ($\boldsymbol{P}$) that represented a random selection of spawning events for each species group. We then used these matrices to quantify numbers and strengths of connections among 314 distinct coral reef complexes across the wider Sunda Banda seascape. Most coral reef complexes represented clusters of multiple 10 × 10 km grid cells, which we assigned by visual examination of natural geomorphological structures of coral reef habitat. However, some natural clusters were subdivided in order to match jurisdictional boundaries of provinces in charge of MPA enforcement. Altogether 225 out of the total of 314 reef complexes were located within the Sunda Banda itself, while 89 represented reef complexes in surrounding areas, which we included to avoid edge effects in connectivity calculations. However, external reef complexes were blocked from protection.

We started developing our optimization problem by parameterizing the connectivity objective function, emphasizing that our goal for the Sunda Banda case study was to design a large-scale network of zoned MPAs rather than a network of multiple small no-take reserves as in idealized scenarios. This emphasis has a significant bearing on the expected ecological function of larval dispersal. Given the large scale of the Sunda Banda seascape it is possible but uncertain whether larval dispersal between MPAs and fished areas over 10s-100s of km will be demographically significant. However, multiple recent studies on population genetic connectivity imply that larval dispersal over such scales can help recolonize collapsed populations or support the productivity of collapsing populations (e.g. Foster et al. 2012). For this reason, we chose to parameterize the two connectivity scaling parameters such that a diverse range of connections rather than a few strong ones are prioritized ($z_\mathrm{I} \approx 0$ and $z_\mathrm{E} \approx 0$). And we aimed to achieve diverse connections not only between MPAs but also from MPAs to putative fishery hotspots, given that most coral reef areas are impacted not only by local and manageable stressors (fishing), but also by global and non-manageable stressors (coral bleaching) (Burke et al. 2012). To achieve this balanced connectivity optimization, we set both the import and export weighting parameters to 0.5.

Given the lack of data on local fishing activities and catch in the Sunda Banda seascape, we parameterized $D_{\mathrm{E},i}$ by approximating relative fishing pressure based on local population densities. For this, we transformed the land population density raster data available from the LSBSA into a feature of points. We then used Inverse Distance Weighting to interpolate resulting data points from land into the ocean, and we then calculated the mean population density per grid cell of coral reef habitat to approximate relative fishing effort. As in idealized scenarios, we assumed that the costs of protecting planning units are uniform so that our optimization was focused entirely on ecological effectiveness and potential fishery benefits. In contrast to idealized scenarios, we set a target of 30% for the protection of coral reef habitat, which matches ambitious conservation goals for the region.

In order to assess the performance of our intended connectivity optimization (balanced design: $w_\mathrm{I} = 0.5$ and $w_\mathrm{E} = 0.5$), we started by using both the site-characteristics and network optimization strategy to identify optimum MPA designs for individual dispersal attributes: (1) local retention ($w_\mathrm{I} = w_\mathrm{E} = 0$), (2) inter-MPA connectivity ($w_\mathrm{I} = 1$, $w_\mathrm{E} = 0$), and connectivity between MPAs and putative fishery hotspots ($w_\mathrm{E} = 1$, $w_\mathrm{I} = 0$). We then contrasted MPA site selection frequencies and MPA network performance. Performance was measured using means across all locations in an open system as a baseline: (1) local retention in MPAs divided by mean local retention across all locations, (2) mean numbers of import connections among MPAs divided by mean numbers of import connections among all locations (multiplied by the proportion of MPAs), (3) mean numbers of export connections weighted by relative fishing effort at export destinations relative to the corresponding mean across all locations (multiplied by the proportion of fished locations). Performance values larger than 1 indicated that MPA designs were better than random (i.e. better than an ad-hoc selection of individual MPAs). All optimizations were based on 100 runs, including all dispersal matrices for different spawning events and species groups.

Following this connectivity-focused part of the analysis, we then used outcomes from balanced network optimizations to identify a single best MPA network that incorporated estimates of general MPA effectiveness. Estimates of general MPA effectiveness were calculated based on five published data layers that specify anthropogenic stressors throughout the Coral Triangle (Burke et al. 2012). Our own approximation of relative fishing effort based on population densities on land was used as a sixth data layer. Local stressors that we considered to be manageable by MPAs included “overfishing, illegal and unreported fishing”, “coastal development”, and “other human activities” (the latter of which represented by our population density layer). Stressors which we considered to be non-manageable by MPAs included “marine pollution” (local), “past coral bleaching” (global), and “future heat stress” (global). To derive a single metric from these data, we firstly normalized each layer to a maximum value of 1. We then subtracted mean non-manageable from mean manageable stress to calculate a single metric of relative MPA effectiveness. The resulting metric assumes that MPAs will have the greatest positive effect in places that are likely to be impacted by manageable stressors, but which are unlikely to be or become impacted by non-manageable stressors. However, the MPA effectiveness metric does not account for possible interactions between stressors, implicitly assuming that associated impacts are additive and independent.

To provide an example of how two (or more) management objectives, such as MPA network effectiveness and connectivity, can be reconciled, we used the Sunda Banda case study with a 30% coral reef habitat protection target and identified a single, highest-scoring, integrated MPA network design. We used the following objective function: $T = E + CSM\ C$, which allowed us to maximize total MPA network performance metric T while adapting the CSM to explore trade-offs between expected effectiveness E and connectivity C. The performance of alternative MPA designs was assessed against maximum scores for E and C, which we calculated as the highest possible mean effectiveness of MPAs that cover 30% of coral reef habitat (E), and the highest (theoretically) possible balanced connectivity score of MPAs that cover 30% of coral reef habitat (C). We then contrasted E and C for increasing values of the CSM (range: 0-1000), identifying the single best MPA network design by determining the first CSM value that yielded lower relative gains in C than relative losses in E. To illustrate the performance of two alternative MPA design strategies, we also calculated C and E for (1) a single best MPA network that maximized 30% of coral reef habitat per unit area; and (2) 1000 networks of randomly placed MPAs that covered 30% of all coral reef habitat. For convenience, and because outcomes were insensitive to the type of optimization procedure applied, we used a greedy optimization approach to implement this final set of analyses. In contrast to simulated annealing, which was used for all previous optimizations and which is implemented in Marxan (Possingham et al. 2000, Ball et al. 2009), the greedy approach assessed performance metrics *E* and *C* for all currently unprotected locations, sequentially selecting the highest scoring areas as MPAs until the combined MPA network covered 30% of coral reef habitat.

We note that the calibration procedure described above assumes approximately equal importance of the two management objectives (MPA effectiveness and connectivity). The same type of trade-off analysis can be used also if one management objective is more important than the other. For example, the same general procedure for *CSM* calibration could be used to integrate a connectivity objective into standard Marxan applications (which minimize a “cost” to represent conservation features in MPAs). The trade-off analysis could then explore how much more it will cost to optimize larval dispersal across the MPA network. Additional management objectives, such as expected MPA effectiveness, could be integrated into such an optimization problem by either integrating estimates of local MPA (in)effectiveness as a “cost” into equation 6, or by adding an independent performance metric *E* with its associated modifier (*ESM*). The latter case would require a trade-off analysis that contrasts three performance metrics (costs, effectiveness and connectivity) in order to achieve desirable calibrations of both the *CSM* and *ESM*.

Results

Relationships between local larval retention, larval import and larval export in simulated data sets followed our general expectations. That is, local retention showed a generally negative correlation with larval import and a generally positive correlation with larval export. Larval import and larval export were generally negatively correlated. However, all three of these expected relationships were significant only under strong and largely diffusive connectivity (the “hotspots” scenario), while under widespread isolation of reef areas (the “patchy” scenario) these expected relationships were either weak or even reversed (Appendix S1: Table S2, Fig. S3).

Reef area provided a useful proxy to estimate dispersal attributes in different locations, showing a generally positive relationship to local retention, a generally negative relationship to larval import, and a generally positive relationship to larval export. Again, however, all three correlations were significant only under strong and diffusive connectivity (Appendix S1: Table S2, Fig. S3).

Idealized connectivity scenarios

The first idealized management scenario, which aimed for maximum retention in reserves under strong but manageable local stress, revealed a similarly high performance for all three systematic MPA designs, rebuilding recruitment in reserves from initially only 10% to minimally 51% (low density-dependent mortality of larvae) and maximally 99% (high density-dependent mortality of larvae) of unfished levels (Fig. 3a-c). Differences between dispersal and habitat-based optimizations were not strong, but dispersal-based MPA designs outperformed habitat-based designs under all dispersal conditions. As expected for local retention, as a static attribute, the site-characteristics and network based optimization strategy revealed identical outcomes. Random MPA designs (ad-hoc selections of MPAs) were least effective, but sufficient to rebuild recruitment in protected populations to minimally 27% of unfished levels, while also holding the capacity to achieve optimal MPA designs by pure chance.

The second idealized management scenario, which aimed to balance local larval retention and larval export to fishing grounds, revealed dispersal-based MPA designs that consistently and substantially outperformed both habitat-based and random MPA designs (Fig. 3d-f). Under both “advective” and “hotspots” dispersal conditions, maximum habitat MPA designs achieved about 3 times higher recruitment into fisheries compared to an open system without any protection, but benefits of this magnitude were comparable to the median achieved by random MPA designs (Fig. 3d and f). Under “patchy” dispersal conditions, maximum habitat MPA designs revealed lower recruitment into fisheries than without any protection, mostly even causing complete recruitment failure (Fig. 3e). Median recruitment into fisheries under random MPA designs was up to 3 times higher than without any protection. However, possible outcomes under random MPA designs were highly variable, ranging from optimum fishery benefits (all dispersal conditions) to complete fishery collapse (“advective” and "patchy") or near-complete fishery collapse ("hotspots"). Dispersal-optimized MPA designs, in contrast, increased the number of recruits available to fishers under any dispersal condition. Compared to an open system without any protection, the network strategy recovered fisheries to minimally 36% ("patchy") and maximally about 80% ("advective" and "hotspots") of the theoretical optimum recruitment. This was equivalent to about 5 times higher numbers of recruits available to fishers compared to unprotected conditions, and about 2 times higher recruitment available to fishers compared to habitat-based MPA designs. The network optimization achieved consistently higher fishery benefits than the site-characteristics strategy, but the magnitude of differences was generally low.

The last idealized management scenario, which aimed to achieve meta-population persistence under local stress and severe, non-manageable disturbances, revealed that dispersal-optimized MPAs can help rebuild meta-population recruitment from initially close to 0% to minimally 25% and maximally 84% of unfished conditions (Fig. 3g-i). In contrast, neither habitat-based nor the majority of random MPA designs achieved any notable recovery of meta-population recruitment. The performance of the site-characteristics and network-based dispersal optimization strategy was very similar again, with both strategies achieving consistently and comparably higher total recruitment than even the best randomly designed MPAs.

Sunda Banda seascape

In the Sunda Banda case study, as in idealized scenarios, the network-based dispersal optimization revealed consistently higher MPA performance than site-based optimizations. Optimum network-based MPA designs achieved 2.2 times higher local retention in MPAs, 2.4 times higher inter-MPA connectivity, and 1.5 times more export connections between MPAs and putative fishery hotspots than expected by chance. For local retention, these results were largely consistent while MPA performance in terms of both import and export connectivity revealed substantial variation across simulated dispersal events and species groups (Fig. 4, Appendix S1: Table S3). Priority locations to achieve maximum local retention in MPAs were distributed across the entire study area (Fig. 4a). In contrast, priority locations to achieve maximum connectivity among MPAs were situated within a relatively small connectivity hub between latitudes 5-9°S and longitudes 119-127°E (Fig. 4c). Priority locations to achieve maximum export connectivity between MPAs and putative fishery hotspots were also concentrated in this region, but did comprise other areas too (Fig. 4e).

Clearly, higher connectivity for species groups with the most frequent spawning events and longest pelagic larval duration was associated with greater benefits from systematic MPA design (Appendix S1: Table S3). However, spatial patterns of connectivity were largely consistent such that priority locations did not vary much by species group (Appendix S1: Fig. S4-S6).

MPA performance under the balanced optimization for all dispersal attributes and simulated dispersal events was intermediate, ranging between outcomes expected for random and those observed for individually optimized MPA designs (Fig. 5). Conflicts in the prioritization of import and export connectivity between and from MPAs appeared to be low, but prioritizing either import or export connectivity was associated with a direct trade-off in the level of local larval retention within MPAs (see Fig. 4). The performance and spatial configuration of balanced MPA designs showed a high similarity again regardless of whether the site-characteristics or network-based optimization strategy was used. Consistently, both strategies identified high priority MPA locations off southern Sulawesi, between Sulawesi, northern Flores and northern Sumbawa, as well as in the Solor-Alor region and around Ambon. Most of these areas are situated in the centre of the Sunda-Banda seascape (Fig. 5).

Integrating management objectives for the likely effectiveness of local MPAs and the network-based dispersal optimization as part our final set of analyses, we found that trade-offs in MPA performance were low. The single best MPA network design achieved a near-optimal connectivity performance score (98%) and 87% of maximum effectiveness (Appendix S1: Fig. S7). The highest priority locations for MPA placement were found to be situated around south-eastern Sulawesi, between Sulawesi and northern Flores, in northern Sumbawa, around Solor-Alor, around Wetar, in south-eastern Buru, and around Ambon. Some of these priority areas fall within the boundaries of official marine parks, such as the Takabonerate National Park, the Wakatobi National Park, and the Bankiriang Wildlife Reserve (Fig. 6). However, other priority areas are either not yet or not yet fully protected. Primarily, this includes a wide stretch of the northern coastline of Flores, the island of Wetar as well as the eastern side of Ambon and southern side of Buru. Specifically because large priority areas around Buru and Ambon met desirable dispersal characteristics in terms of both retention and export to putative fishery hotspots, they represent candidate sites for future MPA network extensions.

Discussion

Several recent studies have highlighted the importance of integrating realistic estimates of larval dispersal into the design of networks of marine reserves or MPAs (Gaines et al. 2003, Costello et al. 2010, Watson et al. 2011, Green et al. 2015). Yet, there is a lack of quantitative approaches that can be applied by marine spatial planners to do so while achieving increasingly diverse management objectives. The two MPA design strategies that we have presented here are sufficiently flexible to explore regional trade-offs (if any) between local larval retention, larval import to and larval export from protected locations. Some of these primary dispersal attributes have either directly or indirectly been considered in previous MPA design approaches (e.g. Beger et al. 2010, Watson et al. 2011, White et al. 2014). However, the integration of all three, as well as of both the strength and diversity of dispersal connections, into a single objective function is novel and should be broadly applicable for both biodiversity conservation and fisheries management.

Our findings suggest that explicit consideration of larval dispersal will be least important if connectivity is diffusive and strong (most closely reflected by the “hotspots” scenario), but that it can be critical under severe disturbance, if patch isolation is widespread, or if larval transport is highly asymmetric (Gaines et al. 2003). Both our “patchy” and “advective” connectivity matrices were based on validated ocean current data, known spawning times, and realistic early life history characteristics of an important fishery species (Beger et al. 2015). Our outcomes highlighted that, specifically in these two cases, meta-population persistence was uncertain and fisheries potentially less than half as productive if MPAs were designed at random or based on a maximum habitat strategy as opposed to our dispersal optimization approach.

Notwithstanding such benefits of systematic MPA design, it is important to note also that in most overfished and poorly regulated systems even random protected area placement is likely to support the persistence or rebuilding of populations and associated fisheries. Protection should therefore be encouraged even if larval dispersal information is not currently available or highly uncertain (Halpern and Warner 2003, Halpern et al. 2006, Jones et al. 2007). Specifically under predominately diffusive connectivity, simply maximizing habitat area in locations that would benefit most from protection should deliver system-wide increases in larval supply and productivity. However, a more targeted support of fished locations through strong and diverse subsidies of larvae from protected areas is likely to benefit strongly from explicit considerations of local dispersal dynamics. The magnitude of associated benefits is difficult to generalize, but our finding of about twice the number of recruits available to fishers compared to habitat-focused MPA designs indicates a potentially critical importance for local food supply and fisher livelihoods.

The site-characteristics and network strategy were similarly efficient in ensuring higher fishery benefits than habitat-focused and random MPA designs. Nevertheless, these two strategies are based on different optimization procedures. The site-characteristics strategy can be integrated more easily with MPA designs based on generic guidelines (Roberts et al. 2003a, Roberts et al. 2003b, Green et al. 2014) or Marxan applications based on standard problem formulation (Possingham et al. 2000, Ball et al. 2009). Its weakness is that it does not consider system-wide larval supply under any given MPA configuration. The network optimization strategy, in contrast, recalculates dispersal during each optimization step, directly considering how larval transport to and from all locations is impacted by changes in the protection status of any single one of these locations. The network strategy also prevents simultaneous selections of important larval sources for fishing grounds that are themselves important sources for other fishing grounds. Due to these characteristics, network-based optimization is preferable, even if more computationally demanding and difficult to integrate with site feature based MPA designs.

Clearly, uncertainty about the predicative capacity of larval dispersal simulations is often considerable (Largier 2003, Cowen and Sponaugle 2009). Few biophysical models have been explicitly tested with known dispersal trajectories (e.g. Sponaugle et al. 2012), and their predictions cannot generally be expected to match field measurements (Marshall et al. 2010). However, for well-studied systems, such as the Great Barrier Reef, there is an increasingly broad agreement between empirical data and simulated larval dispersal, including levels of self-recruitment and directionality in dispersal (Jones et al. 1999, James et al. 2002, Bode et al. 2006, Harrison et al. 2012). The use of simulated dispersal patterns for systematic MPA design is thus likely to increase. Encouragingly, even inexperienced practitioners are able now to generate and use dispersal matrices by accessing publicly available modelling tools to perform sets of locally representative dispersal simulations. For example, this is possible by using the global connectivity modelling function of the Marine Geospatial Ecology Tools package (MGET, mgel.env.duke.edu/mget) (Roberts et al. 2010), or by using the Australian

Marine Connectivity Interface (ConnIe) (Condie et al. 2005, Condie and Andrewartha 2008), which now covers a broad region around Australia, New Zealand, south-east Asia and Micronesia, as well as the Mediterranean Sea (ConnIe 2, www.csiro.au/connie2/). Both tools are based on widely published dispersal models, well-documented and user-friendly.

Major challenges to use simulated dispersal patterns for systematic MPA design include not only how explicit connectivity objectives are best integrated with other management goals, but also to account for potentially substantial variation in dispersal among species and through time (e.g. Hogan et al. 2012). We have dealt with this complexity here by optimizing MPA designs based on various simulated dispersal events, and by treating them as equally important. The result was a network of MPAs that achieved the best average dispersal outcomes. For the Sunda Banda case study, this strategy was acceptable given that priority locations for different species groups were largely consistent. In other cases, more substantial variation in site selection frequencies might be reduced by using species-group-specific parameterizations (e.g. focusing on local larval retention in MPAs for the least threatened and on a balanced dispersal parameterization for the most threatened taxa). Alternatively, species groups could be weighted by some measure of vulnerability or fisheries importance.

While there is a clear need for greater validation of dispersal models, our analyses indicate that under a broad range of connectivity scenarios management outcomes can be improved if dispersal information is incorporated into systematic MPA design. Particularly if connectivity is highly asymmetric, doing so could be essential to ensure any conservation or fisheries benefit. Directional larval transport in the California current system is the most well-known example of such highly asymmetric connectivity, triggering seminal research into the influence of larval dispersal on marine meta-population dynamics (Roughgarden et al. 1988, Possingham and Roughgarden 1990, Shanks and Eckert 2005), as well as on marine reserve network design (Gaines et al. 2003, Shanks et al. 2003).

In conclusion, our findings demonstrate the feasibility of a novel MPA design approach for connectivity optimization, which can systematically support the likely persistence and productivity of marine populations. Importantly, our approach does not require assumptions about persistence thresholds or demographic importance (which are generally unknown), and it achieves consistently high management performance regardless of local dispersal patterns and the degree of density-dependent mortality after settlement. Specifically because the approach is both transparent and flexible, future applications should help marine spatial planners to reconcile multiple, potentially conflicting management objectives, including biodiversity conservation inside as well as fisheries subsidies outside of protected area boundaries. The first outputs from our approach are currently used to help conservation priority area setting in Indonesia.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/eap.xxxx/suppinfo

Tables

Table 1. Implications of the sources of recruitment for marine protected area design. Note that the remaining two out of nine possible combinations under “Recruitment” do not exist, because populations would not exist. “Either” under “Vulnerability” highlights locations that are not vulnerable to either local or global threats. “Both” under “Good location to protect?” means that protection benefits conservation (Cons.) and fisheries.

Recruitment			Vulnerability			Good fishing area?	Good location to protect?		
Self	Import	Export	Local	Global	Either		Cons.	Fishery	Both
Yes	Yes	No	No	No	No	Yes	Yes	No	No
No	Yes	No	No	Yes	Yes	Yes	No	No	No

Yes	No	Yes	Yes	No	Yes	No	Yes	Yes	Yes
Yes	Yes	Yes	No	No	No	Yes	Yes	Yes	Yes
No	Yes	Yes	No	Yes	Yes	Yes	Yes	Yes	Yes
Yes	No	No	Yes	No	Yes	No	Yes	No	No

Figures Legends

Figure 1. Illustration of the conceptual framework and parameterization of our marine protected area design approach (a). The approach allows users to reconcile multiple dispersal attributes in support of both protected and unprotected populations by adapting the connectivity weighting (*w*), scaling (*z*) and desirability (*D*) parameters. The lines between boxes in (a) exemplify a balanced optimization as followed in our Sunda-Banda case study ($w_I = w_E = 0.5$). A hypothetical seascape (b) is used to give examples of maximum priority locations (c-f) under alternative management objectives. In both e and f export destinations *j* are ignored if they are not fished ($D_{E,j} = 0$). The centre location stands out as a candidate site for protection, receiving maximum priority under all management objectives (c-f). Note that objectives for conservation and fisheries management are not necessarily different, including, for example, higher productivity (through high larval supply) or long-term persistence (through highly diverse larval sources) of unprotected populations.

Figure 2. Connectivity matrices used to investigate the performance of alternative marine protected area design scenarios: (a) “advective” connectivity characterized by comparatively strong unidirectional flow of larvae, (b) “patchy” connectivity characterized by widespread isolation of reef areas, and (c) “hotspots” connectivity characterized by a few influential connectivity hubs and largely diffusive flow of larvae. Connection strengths are based on absolute numbers of larvae dispersing between 50 locations. Data are capped and normalized to 1 based on regional maxima.

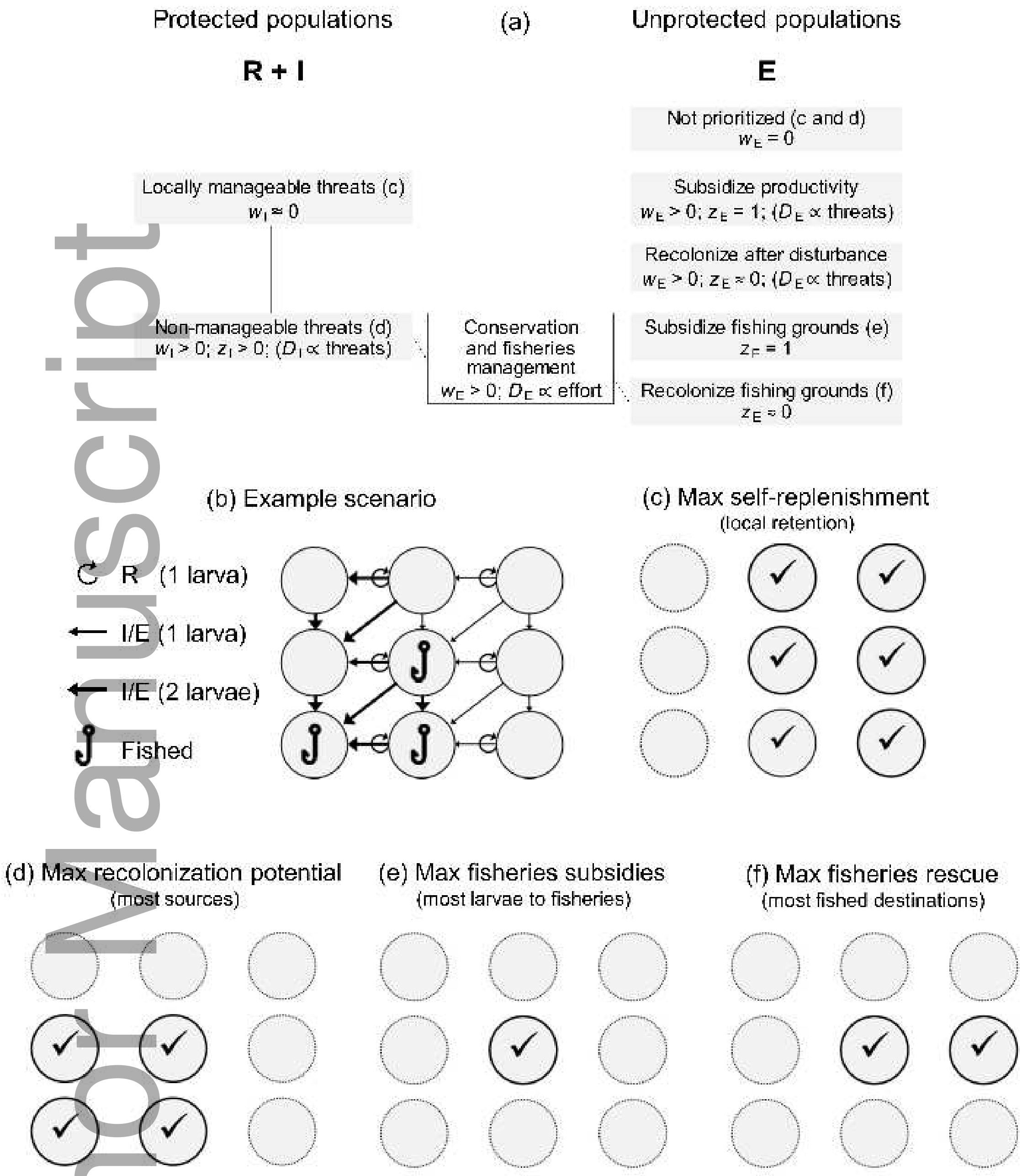
Figure 3. Marine reserve network performance under variable dispersal conditions, threats, and management objectives. Results show numbers of recruits (*R*) relative to post-settlement density-dependent mortality of larvae, ranging from very high (small $h = 0.3$) to very low (large $h = 0.95$). The management focus was to maximize local larval retention (upper panel, a-c), to balance local retention and fishery rebuilding (middle panel, d-f), and to balance local

retention within and dispersal between protected locations under severe and non-manageable disturbance (lower panel, g-i). The grey area highlights the complete range and the grey dotted line the median of outcomes across 100 randomly designed reserve networks. R_0, unfished recruitment; R_{MER}, recruitment delivering maximum excess recruitment. See methods for details.

Figure 4. Site selection frequencies and Marine Protected Area (MPA) network performance on coral reefs in the Sunda Banda seascape in Indonesia yielding optimum dispersal outcomes. MPA network performance in bar graphs is expressed as means ± SD across all simulated dispersal events. All results are based on the network optimization strategy, yielding highest local larval retention within MPAs (R_{MPA}) (a) and (b), the highest connectivity between MPAs (I_{MPA}) (c) and (d), and the highest connectivity between MPAs and putative fishery hotspots (E_{Fished}) (e) and (f). See methods for details.

Figure 5. Site selection frequencies of Marine Protected Area (MPA) network designs on coral reefs in the Sunda Banda seascape yielding balanced connectivity performance. MPA network performance in bar graphs is expressed as means ± SD across all simulated dispersal events. The upper panel (a-b) refers to the site-characteristics and the lower panel (c-d) to the network based optimization strategy. Both strategies were parameterized to balance local larval retention within MPAs (R_{MPA}), diverse import connections between MPAs (I_{MPA}), and diverse export connections from MPAs to putative fishery hotspots (E_{Fished}). See methods for details.

Figure 6. Priority locations for marine protected area (MPA) placement on coral reefs in the Sunda Banda seascape, Indonesia. The MPA network design is based on the balanced connectivity optimization objective (see Fig. 5c and d), but integrates the likely effectiveness of MPAs in different locations (see methods for details). High priority MPA locations are highlighted in red, covering 30% of coral reef habitat. Green lines indicate the boundaries of officially declared MPAs. Black dots are the centroids of coral reef areas used for larval dispersal simulations (n = 225). Blue lines represent the probability that a larva of any simulated fishery species disperses between a given pair of reef areas (dark blue: 1 in 1,000, light blue: 1 in 10,000). In (a), connections represent larval import into MPAs. In (b), connections represent larval export from MPAs to fished areas. Am, Ambon; Bu, Buru; SA,



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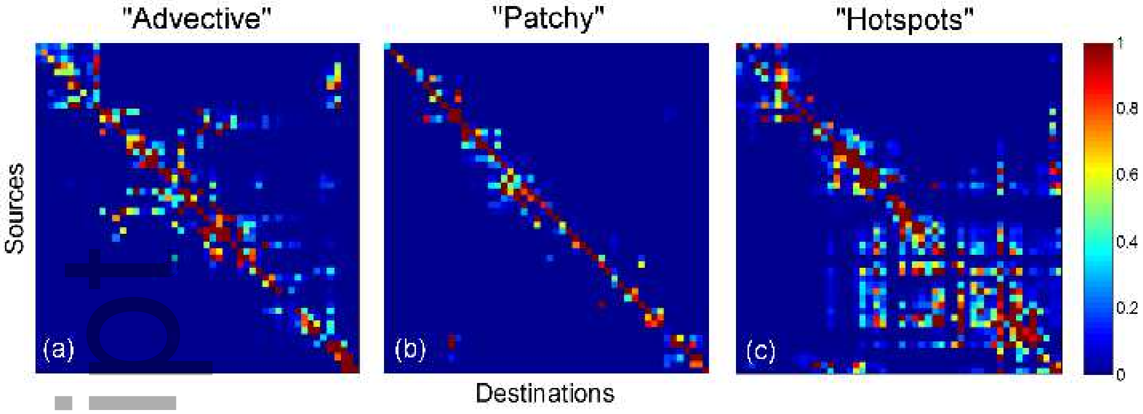

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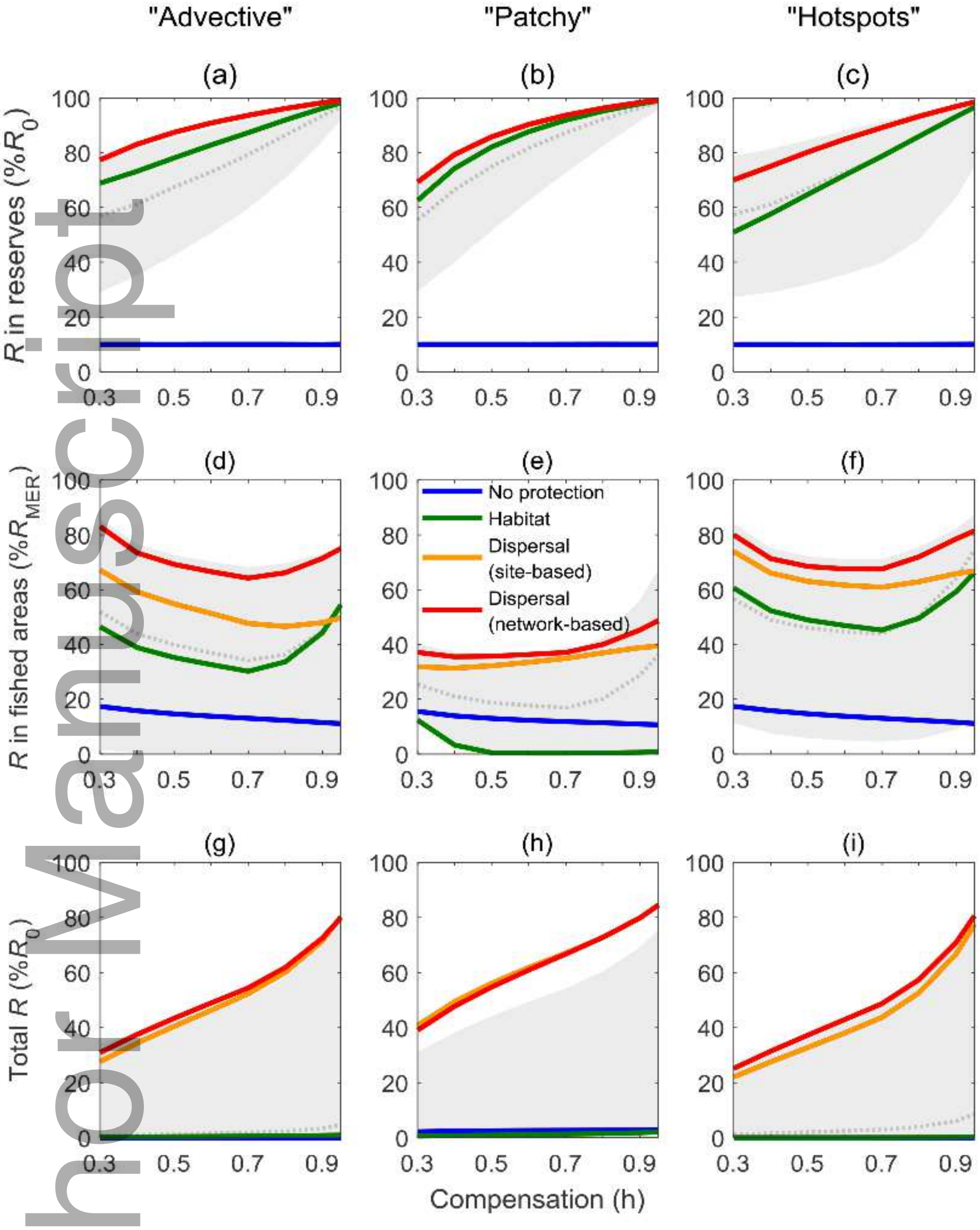

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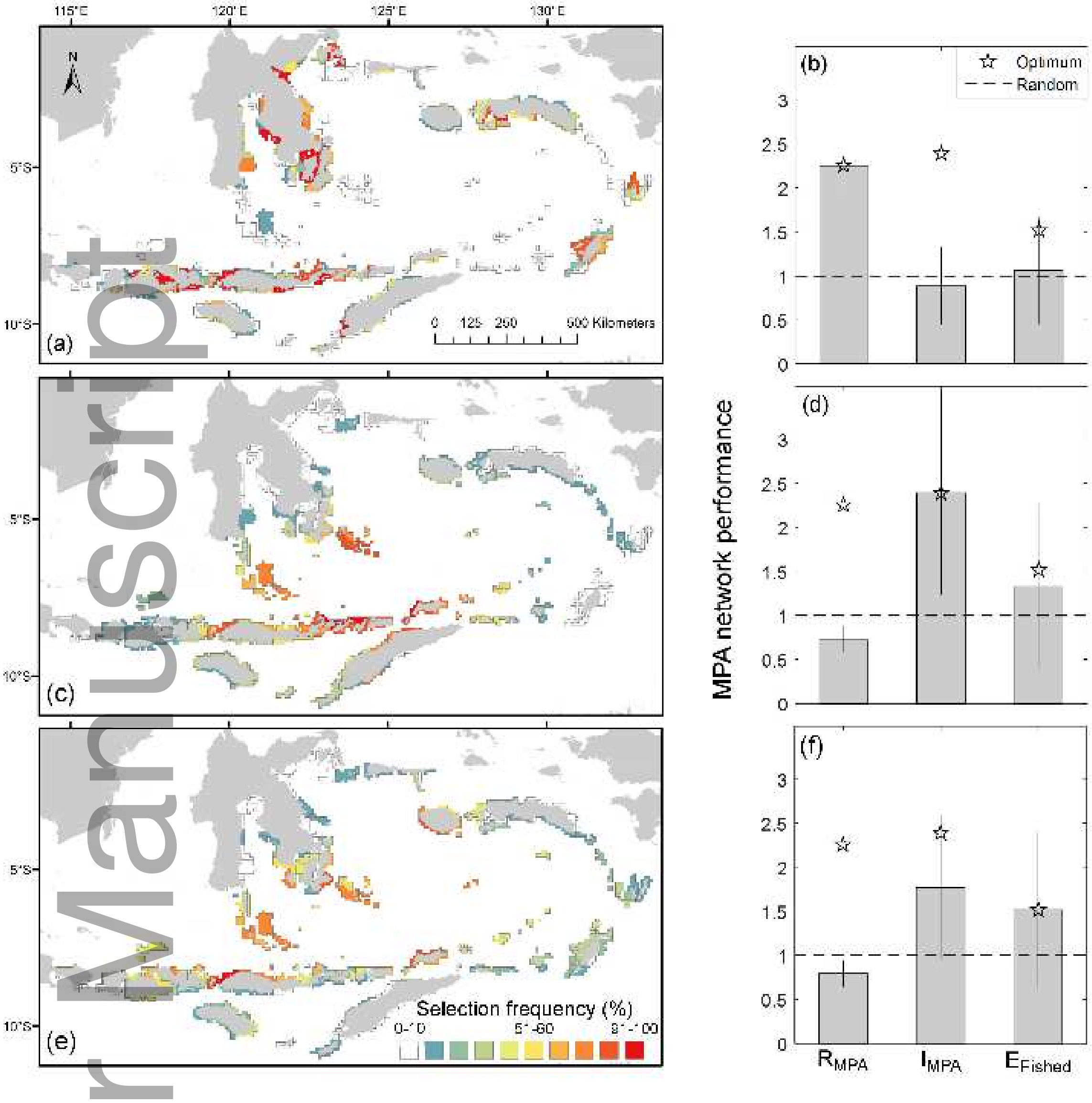

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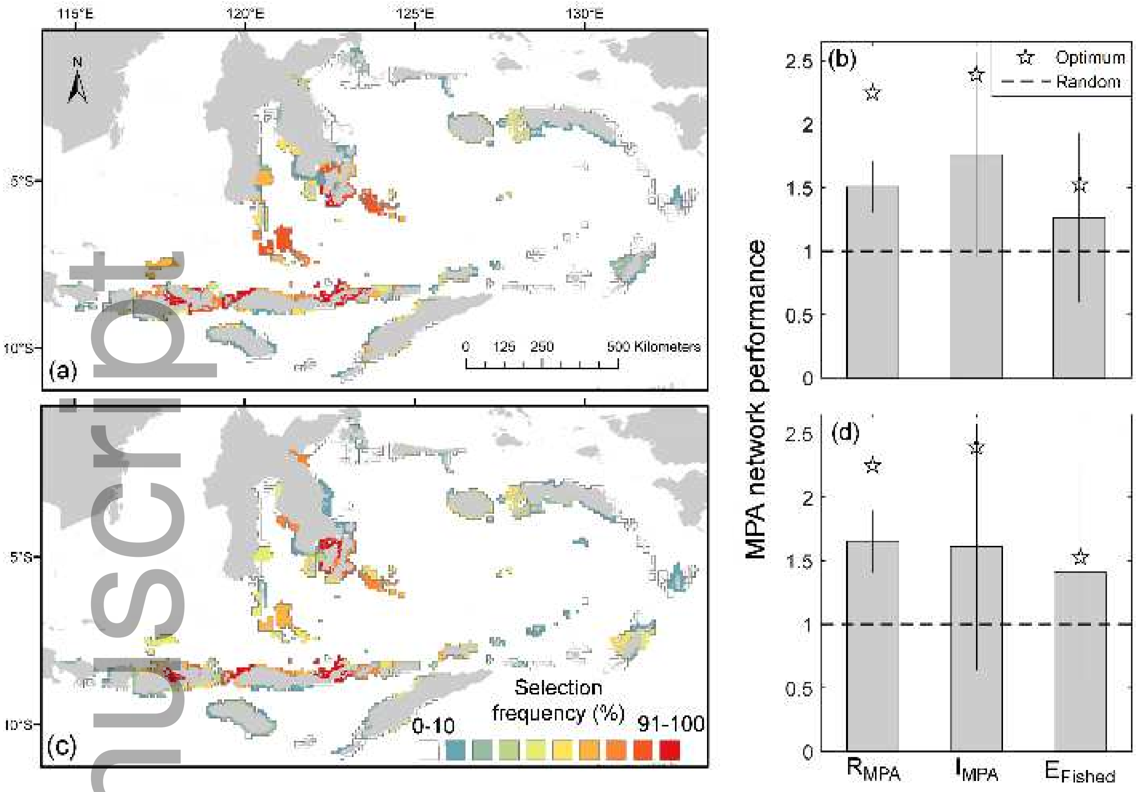

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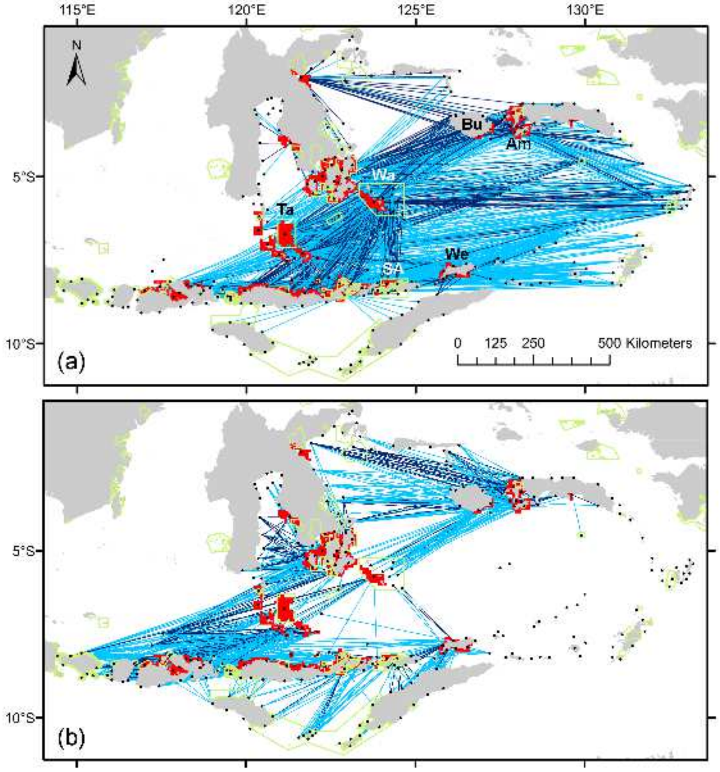

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