

# Siting marine protected areas based on habitat quality and extent provides the greatest benefit to spatially structured metapopulations

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**Abstract.** Connectivity and its role in the persistence and sustainability of marine metapopulations are attracting increased attention from the scientific community and coastal resource managers. Whether protection should prioritize the connectivity structure or demographic characteristics of a given patch is still unclear. We design a three-stage population model to analyze the relative importance of sources, sinks, quality and extent of juvenile and adult habitat, and node centralities (eigenvector, degree, closeness, and betweenness) as a basis for prioritizing sites. We use a logistic-type stage-structured model to describe the local dynamics of a population with a sessile adult stage and network models to elucidate propagule-exchange dynamics. Our results show that the coupled states of habitat extent and quality, which determine population carrying capacity, are good criteria for protection strategy. Protecting sites on the basis of sources, sinks, or other centrality measures of connectivity becomes optimal only in limited situations, that is, when larval production is not dependent on the adult population. Our findings are robust to a diverse set of larval pathway structures and levels of larval retention, which indicates that the network topology may not be as important as carrying capacity in determining the fate of the metapopulation. Protecting extensive, good quality habitat can help achieve both conservation and fisheries objectives.

**Key words:** connectivity; habitat extent and quality; habitat restoration; marine protected area; marine protected area network; marine reserve; metapopulation; patch dynamics; source and sink.

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## INTRODUCTION

A metapopulation is a network of spatially separated populations that interact at some level (Levins 1969, 1970). Many species of marine fish and invertebrates have a bipartite life cycle, with a dispersing pelagic larval stage and benthic juvenile–adult stages that are more sedentary (Roughgarden et al. 1988). Therefore, this system corresponds to a metapopulation of reef patches

connected via larval dispersal (e.g., Man et al. 1995, Sale 2002, Sale et al. 2006). The dispersal can occur over great distances (Kinlan and Gaines 2003), and the chaotic nature of ocean currents leads to asymmetric dispersal of larvae (Siegel et al. 2008).

One of the objectives of conservation biology and fisheries management is to prioritize marine areas or patches that are crucial to the viability of a metapopulation (Visconti and Elkin 2009). A patch's contribution to a fishery is attributed to

the connectivity structure of the metapopulation, the persistence of the metapopulation, the extent of the habitat, and habitat conditions, which reflect recruit and adult survivorships (Gaines et al. 2010). However, the relative importance of the connectivity structure and intrinsic or demographic characteristics of a patch (e.g., habitat quality and extent) is a topic of ongoing investigation (Figueira and Crowder 2006).

Seminal works on metapopulation dynamics suggest that habitat size and isolation are sufficient to explain the variation in the population sizes of patches (e.g., Moilanen and Hanski 1998). Others have highlighted the role of connectivity, in addition to habitat size, in population persistence (e.g., Isaak et al. 2007). Models have shown that protection should prioritize areas with high connectivity, or “hubs” (e.g., Kininmonth et al. 2011). After all suitable hubs have been protected, isolated sites should be protected to increase the connectivity of the system. Asymmetry in the level of connectivity negatively affects metapopulation persistence (Bode et al. 2008). Models that consider local population dynamics have also found that connectivity may be more important than habitat quality as a selection criterion for protection (i.e., Watson et al. 2011, Berglund et al. 2012). However, some studies have indicated that habitat quality may be more important than connectivity for the persistence of metapopulations (e.g., Wynne and Côté 2007, Carson et al. 2011, López-Duarte et al. 2012). High-quality habitats may support larger populations through a number of demographic processes, including higher survival of either juveniles or adults (Tupper and Boutilier 1997). Nevertheless, the role of habitat quality in determining population viability is increasingly recognized (e.g., Hanski 1998, Thomas et al. 2001, Fleishman et al. 2002, Jaquiéry et al. 2008, Figueira 2009, Berglund et al. 2012, Griffen and Norelli 2015). A high-quality and extensive habitat patch may benefit from low extinction rates driven by increased survival and fecundity, as well as higher colonization rates driven by enhanced settlement and recruitment (Griffen and Drake 2008, Jaquiéry et al. 2008).

In a marine reserve context that involves siting a single reserve, the current rule of thumb is to protect the areas that are larval sources and/or larval sinks (Crowder et al. 2000, Gaines et al.

2003). The protection of a source site may compensate for a loss of fisheries harvest in both reserve and non-reserve areas (Christie et al. 2010, Gaines et al. 2010). Population sinks, on the other hand, may contain numerous individuals because of the large influx of recruits from sources; when local reproduction in sink sites is insufficient to offset local mortality, the sink population may not sustain itself in the absence of sources. Therefore, population management based on sinks may be a cause for serious concern (Pulliam 1988). While isolated reef patches or sites with a low net influx of recruits can still be resilient (Gilmour et al. 2013), local management will be very important (Roberts 1997).

The number of juveniles and adults that a site can accommodate is often regulated by habitat extent or availability (e.g., Mumby et al. 2004, Nagelkerken et al. 2012). Habitat quality also affects the size of the population (Roberts and Ormond 1987, McClanahan 1994, Rodwell et al. 2003, Shima and Osenberg 2003) by regulating juvenile and adult survivorship (e.g., Tupper and Boutilier 1997, Wynne and Côté 2007, Watson et al. 2011). Juveniles and adults of some species may utilize the same habitat (e.g., coral reef fish species such as pomacentrids and chaetodontids; Wilson et al. 2008), while others may use different habitats in their various life stages (e.g., nursery species such as some groupers; Eggleston 1995, Nagelkerken et al. 2001, Mumby et al. 2004, Mamaug 2011). In the absence of nursery habitats such as mangroves, both juvenile and adult nursery species are either absent or present in low densities (Nagelkerken et al. 2002).

Here, a three-stage population model was formulated to investigate the relative importance of sinks, sources, habitat extent, habitat quality, and network centralities (eigenvector, degree, closeness, and betweenness) in determining the viability of a fish population with a sedentary adult stage and a pelagic larval stage. Three complex network models (i.e., Watts–Strogatz, Barabási–Albert, and Erdős–Rényi) were used to create multiple synthetic metapopulation connectivity structures. Studies have shown that larval connectivity patterns in nearshore marine populations exhibit small-world characteristics, which are the properties of a Watts–Strogatz network (Kininmonth et al. 2010, 2011, Watson et al. 2011). The network structure dictates

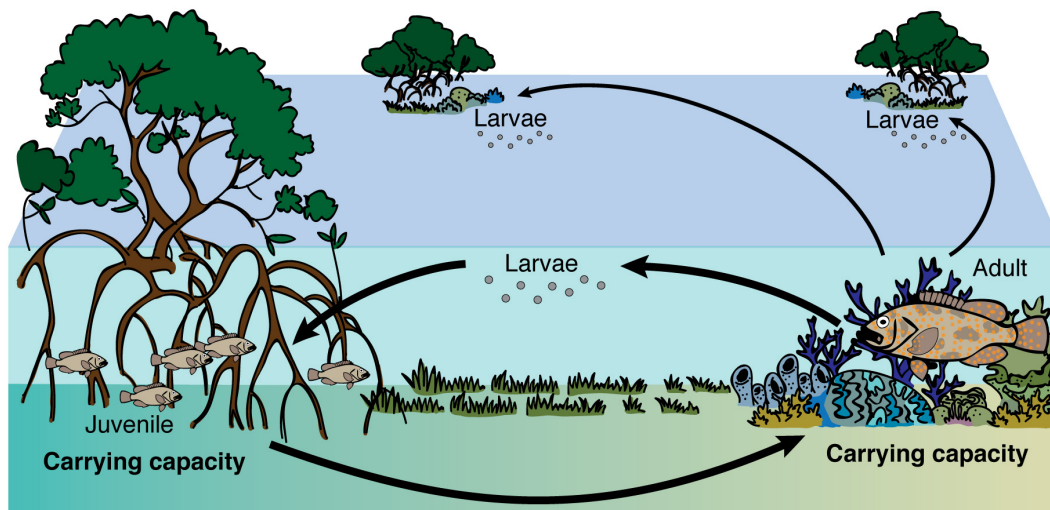


Fig. 1. The three-stage population model: larval stage, juvenile stage, and adult stage. The figure shows three metapopulation sites connected by larval dispersal.

propagule-exchange dynamics. Total fish population (adult fish abundance) was used as a metric for comparing protection strategies. We aim to address the following questions: (1) Which network metrics or properties of sites should serve as a basis for prioritizing sites for protection: sources, sinks, network centralities, habitat extent, habitat quality, or some combination of these factors? and (2) How will the results vary for different levels of self-recruitment and connectivity structures? Answers to these questions will allow conservation and management agencies to prioritize and target management efforts.

## METHODS

We consider a three-stage population model comprised of larval, juvenile, and adult fish populations (Fig. 1). The adults are spawning populations, and the larvae disperse to other connected sites. Local larval retention is permitted. The larvae are recruited to the juvenile population, and the juvenile population is recruited to the adult population. Hence, the replenishment of the adult population is directly dependent on the cohorts of individuals in the nursery habitat (Verweij et al. 2008, Jones et al. 2010).

### Generating complex networks

We use complex networks to generate all possible larval pathways and enable the analysis of

their effect on the metapopulation. Sites (subpopulations or patches of habitats) and connections are represented by nodes and edges, respectively. Edges are ecological connections between sites and represent propagule dispersal or pathways of material exchange (Urban and Keitt 2001, Watson et al. 2011). Three basic random network models are used: Erdős–Rényi (ER, Erdős and Rényi 1960), Watts–Strogatz (WS, Watts and Strogatz 1998), and Barabási–Albert (BA, Barabási and Albert 1999) (see Appendix S1 for a brief description of the different network structures).

### Local population dynamics

We consider  $n = 100$  nodes, each representing a metapopulation site. Each site has a fish population, as well as juvenile and adult habitats that vary in extent and quality. Reproduction is discrete, which is an appropriate description for many benthic marine species (e.g., reef fish species) with defined reproductive periods (Lockwood et al. 2002). The adult population releases larvae, and the larvae are transported to other sites through the connectivity matrix.

Carrying capacity differs for the juvenile and adult stages of reef fish (Halpern et al. 2005). The difference is particularly marked when the two stages utilize different ecosystems (i.e., ontogenetic habitat movement). The quality (Tupper and Boutilier 1997, Wilson et al. 2008) and extent (e.g., Rijnsdorp et al. 1992) of the nursery habitat

determine the carrying capacity, and thus the size, of the juvenile populations. Similarly, the extent and quality of the adult population's habitat limit the size of the population of adult fish; habitat degradation and loss can negatively affect the natural mortality and productivity of the adult reef fish population (Neudecker 1982, Halpern et al. 2005, Wynne and Côté 2007, Wilson et al. 2008).

The recruitment process from the larval stage to the juvenile stage at site  $i$  is driven by a density-dependent mechanism described by:

$$J_i(t) = \frac{k_i^J(E_i^J, q_i^J) L_i^{\text{total}}}{k_i^J(E_i^J, q_i^J) + L_i^{\text{total}}} \quad (1)$$

where  $k_i^J(E_i^J, q_i^J) = J_{\text{max}} E_i^J q_i^J$ . Juvenile stage carrying capacity ( $k^J$ ) is dependent on both the extent ( $E^J \in [0,1]$ ) and quality ( $q^J \in [0,1]$ ) of the juvenile habitat.  $J_{\text{max}}$  is the maximum possible juvenile population that a metapopulation site can accommodate. A metapopulation site with excellent juvenile habitat extent and quality ( $E_i^J = 1$  and  $q_i^J = 1$ ) will have  $k_i^J = J_{\text{max}}$ .  $L_i^{\text{total}}$  is the amount of larvae that reaches site  $i$ . Three larval production models were used to investigate the sensitivity of the results to the larval production dynamics (see *Larval production models*). Eq. 1 implies that density dependence is negligible at low larval populations.

Assuming that the juvenile stage lasts one time step, the adult population at site  $i$  at time  $t + 1$  is:

$$A_i(t+1) = \frac{k_i^A(E_i^A, q_i^A) \{ [A_i(t) \times \exp(-M_{A_i})] + [J_i(t) \times \exp(-M_{J_i})] \}}{k_i^A(E_i^A, q_i^A) + [A_i(t) \times \exp(-M_{A_i})] + [J_i(t) \times \exp(-M_{J_i})]} \quad (2)$$

where  $M_{J_i}$  is the natural mortality of the juvenile stage, and  $M_{A_i}$  is the natural mortality of the adult population. Eq. 2 has the same functional form as that governing the juvenile population. The adult population carrying capacity ( $k^A$ ) is also a function of the extent ( $E^A \in [0,1]$ ) and quality ( $q^A \in [0,1]$ ) of the adult population habitat:  $k_i^A(E_i^A, q_i^A) = A_{\text{max}} E_i^A q_i^A$ , where  $A_{\text{max}}$  is the maximum possible adult population that a metapopulation site can accommodate. A metapopulation site with excellent adult habitat extent and quality ( $E_i^A = 1$  and  $q_i^A = 1$ ) will have  $k_i^A = A_{\text{max}}$ . The

carrying capacity of juvenile and adult habitats can be improved if additional habitats are introduced through restoration and transplantation, as well as introduction of artificial habitats or improvement of the habitat quality through protection (e.g., marine protected areas, or MPAs).

Changes in habitat patches can alter the landscape of the metapopulation, and habitat destruction and loss are central driving forces in conservation biology (Hanski 1998, Urban and Keitt 2001). To determine the relative importance of a given factor (e.g., sources, sinks, extent and qualities of juvenile and adult habitats, and node centralities) as the basis for selecting areas for protection, we arrange the sites in decreasing order by the factor of interest. We then implement sequential deletion of sites. An optimal strategy should show a declining impact on the stock as less productive, and less important sites are deleted. Deleting sites with the highest juvenile or adult habitat quality, highest juvenile or adult habitat extent, highest outbound connections (source), highest inbound connections (sinks), or other centrality measures (degree, closeness, betweenness, and eigenvalue centrality) should result in a larger decline in the global fish population size. The centrality of a node, which describes the importance of the node in the network, differs for different centrality measures. A node is more central if it has more neighbors (degree centrality), if it can reach other nodes easily (closeness centrality), if the shortest path (shortest number of nodes to cross) between any two nodes disproportionately involves this node (betweenness centrality), and if it is connected to high degree nodes (eigenvector centrality). A source is usually defined as a site where the net export of individuals (larvae) is greater than the net import of individuals, while a sink is defined as a site with the opposite ratio of net export to net import (Cowen and Sponaugle 2009), but here we define sink and source in terms of connections. A high number of inbound connections imply a greater chance of receiving large amounts of larvae from many sources, while a high number of outbound connections mean that larvae are dispersed to many sites. We conduct deletion by setting  $q_i^A = 0$  whenever site  $i$  is selected.

We implement a greedy algorithm to derive the sequence of site deletion that corresponds to the optimal strategy for protection. The greedy

algorithm works by removing sites one by one and measuring the impact of the site removal on the entire metapopulation. A site is defined as the most important when the site's removal results in the greatest decline in total adult fish population of the entire metapopulation. We then arranged the sites in order of decreasing importance. We compare the performance of the strategies based on measurable metrics for protection (e.g., source, sink, habitat quality, habitat extent, etc.) to the performance of the greedy algorithm. The protection strategy is optimal when the ranking of sites for protection corresponds to the ranking generated by the greedy algorithm. We also use the index  $C^{0.5}$  to measure the number of nodes that must be deleted so that the total stock is half of the total virgin adult population (Watson et al. 2011). For this index, a lower number indicates that the protection strategy is more effective in identifying key sites for protection. A lower  $C^{0.5}$  value indicates that fewer sites are needed to be protected in order to capture the most benefit. A  $C^{0.5}$  of 25 means that 25 sites must be protected to ensure that fish biomass does not go below 50% of virgin adult fish population.

We conduct the simulation over 100 population generations that have achieved a steady-state metapopulation. We generate one hundred nodes and assign to them a random juvenile and adult habitat extent and quality. We assign a constant natural mortality of 0.2 for both  $M_j$  and  $M_A$ . We use an initial population of 10 individuals for both the juvenile and adult populations for each site.

#### Network directionality and self-seeding

Reef fish population connectivity is commonly asymmetric between patches because of the advective component of ocean currents. In addition, some level of local larval retention is common. However, the links or edges in the three network models used in this study are bidirectional and there are no self-loops to represent self-seeding or local larval retention. We modify the network models to simulate variable directionality in links and include self-seeding probability. We use  $P$  as the probability that a single connection will be deleted in a bidirectional link;  $P = 1$  means that a link will be deleted (all links are directed), and  $P = 0$  means no links will be deleted (all links are bidirectional).

The level of self-recruitment (locally produced and retained recruits—Botsford et al. 2009) has been measured empirically for only a few species, but studies of coral reef fish species (Pomacentridae and Chaetodontidae) have yielded ranges from 15% to 60% (Jones et al. 1999, Almany et al. 2007). Although self-recruitment is different from local retention (defined as the ratio of locally produced settlement to total locally released larvae; Botsford et al. 2009), Hogan et al. (2012) found that the level of self-recruitment among seven populations of a coral reef fish (*Stegastes partitus*) is consistent in value with the level of local retention. Connectivity matrices from oceanographic models can also be used to estimate the level of local retention for a far broader array of circumstances (e.g., see Mitarai et al. 2008, Cowen and Sponaugle 2009, Watson et al. 2011).

We use four values of local larval retention ( $l$ ): 0% ( $l = 0$ ), 10% ( $l = 0.1$ ), 50% ( $l = 0.5$ ), and 90% ( $l = 0.9$ ). These values indicate the percentage of the total propagules produced by site  $i$  that are retained at site  $i$ . Zero local larval retention is included to evaluate the role of habitat.

The highly asymmetric nature of the simulated connectivity patterns mimics the variable recruitment rates in reef fish metapopulations (Doherty and Fowler 1994).

#### Larval production models

We use three larval production models to test the sensitivity of the protection strategies to the larval production dynamics. In all cases, we do not explicitly model the mortality in the pelagic larval stage.

*Model 1: Larval output distributed equally among connected sites.*—Site  $i$  produces  $A_i L$  larvae where  $A_i$  is the size of the adult population at site  $i$  and  $L$  is the per capita larval production. Some of these larvae are self-recruited. The amount of larvae that are self-recruited at site  $i$  is given by  $l A_i L$  where  $l = \{0, 0.1, 0.5, 0.9\}$  is the level of local larval retention. The rest of the larvae are distributed equally to all connected sites. Here, we used  $L = 100$ , but we also tested for  $L = 10$  and  $L = 1000$  (see Appendix S1). Therefore,  $L_i^{\text{total}}$  in Eq. 1 is the sum of all larvae received by site  $i$  from all sites, including the self-seeded larvae.

*Model 2: Larval production proportional to the number of successful connections and adult*

*population size.*—In Model 1, the larvae produced by site  $i$  (minus the self-recruited larvae) are distributed evenly to all outbound connected sites. This implies that the higher the number of outbound connections, the lower the fraction of larvae distributed to the outbound sites. Therefore, it does not imply that more inbound connections will lead to more larvae. In the field, however, the opposite may occur. The total number of recruits originating from a site depends on the number of sites with successful outbound connections. The vast majority of larvae never recruit to juvenile habitats at any site. Part of this phenomenon can be attributed to larval mortality, but perhaps a larger part is due to the probability of larvae that are competent to settle never encountering juvenile habitat.

Here, the number of larvae produced by site  $i$  scales with the number of outbound connections of site  $i$  and the adult population at site  $i$ . Site  $i$  produces  $u_i A_i L$  larvae, with additional contribution from self-seeding, which are either equal to 0 or  $A_i L$ . The parameter  $u_i$  is the number of outbound connections that site  $i$  has,  $A_i$  is the adult population at site  $i$ , and  $L$  is the per capita larval production. We consider  $L = 1$  and  $L = 1000$  to compare low and high larval production.  $L_i^{\text{total}}$  in Eq. 1 is the sum of all larvae received by site  $i$  from all sites, including the self-seeded larvae.

*Model 3: Larval production proportional to the number of successful connections but not adult population.*—Here, the number of larvae produced by site  $i$  only depends on the number of outbound connections of site  $i$ : Site  $i$  produces  $u_i a_i L_C$  larvae, with additional contribution from self-seeding, which are either equal to 0 or  $a_i L_C$ . The parameter  $u_i$  is the number of outbound connections that site  $i$  has,  $a_i$  is a constant that is equal to 1 if the adult population at site  $i$  is nonzero and is otherwise equal to 0, and  $L_C$  is the level of constant larval production per successful connection. As long as there are adults in a site, a site can supply a constant number of larvae to connected sites. We consider  $L_C = 1$  and  $L_C = 1000$  to compare low and high larval production.  $L_i^{\text{total}}$  in Eq. 1 is the sum of all larvae received by site  $i$  from all sites, including the self-seeded larvae. This larval production model may not have a biological justification but is a useful thought

experiment as it could maximize the impact of connectivity on MPA network design.

## RESULTS

For Model 1, where larval output is distributed equally among connected sites, protection based on metrics of connectivity (i.e., node centralities, source, sink) is suboptimal (Fig. 2). Protection based on preserving high-quality or extensive habitat shows better performance than protection based on connectivity, but this performance is still suboptimal compared with that of the greedy algorithm. For  $J_{\text{max}} > A_{\text{max}}$  (adult habitat limits adult population size), the multiplicative effect of adult habitat quality and habitat extent ( $q^A E^A$ ), which determines adult carrying capacity, follows the same path taken by the greedy algorithm, suggesting that it is the optimal solution (Fig. 2). A protection strategy based on preserving high juvenile habitat carrying capacity ( $q^J E^J$ ) is suboptimal (Fig. 2). The result is opposite when  $A_{\text{max}} > J_{\text{max}}$  (juvenile habitat limits adult population size; Fig. 3; see also Appendix S1: Figs. S5–S8 for a similar case where there is no adult carrying capacity). For this case, a protection strategy based on preserving high juvenile habitat carrying capacity is optimal, whereas a strategy based on preserving high adult habitat carrying capacity is suboptimal.

The performance of protection strategies based on preserving high juvenile habitat carrying capacity ( $q^J E^J$ ) and high adult habitat carrying capacity ( $q^A E^A$ ) for variable  $J_{\text{max}}$  and  $A_{\text{max}}$  is illustrated in Fig. 4a–c. Fig. 4c shows the performance for the strategy of selecting sites on the basis of the limiting habitat, that is, *minimum* ( $q^J E^J$ ,  $q^A E^A$ ). The strategy of preserving sites on the basis of the limiting habitat results to a consistently lower  $C^{0.5}$  values for different combinations of  $J_{\text{max}}$  and  $A_{\text{max}}$ , indicating that it is the optimal protection strategy.

The level of larval retention ( $l$ ) for the three network models considered (WS, BA, ER) has no effect on the resulting protection strategy (Fig. 5a–c,  $J_{\text{max}} > A_{\text{max}}$ ). A protection strategy based on preserving high adult habitat carrying capacity ( $q^A E^A$ ) is an optimal strategy as it has the same  $C^{0.5}$  value as the greedy algorithm. The strategy based on the minimum of  $q^J E^J$  and  $q^A E^A$  is also an optimal strategy. These results hold

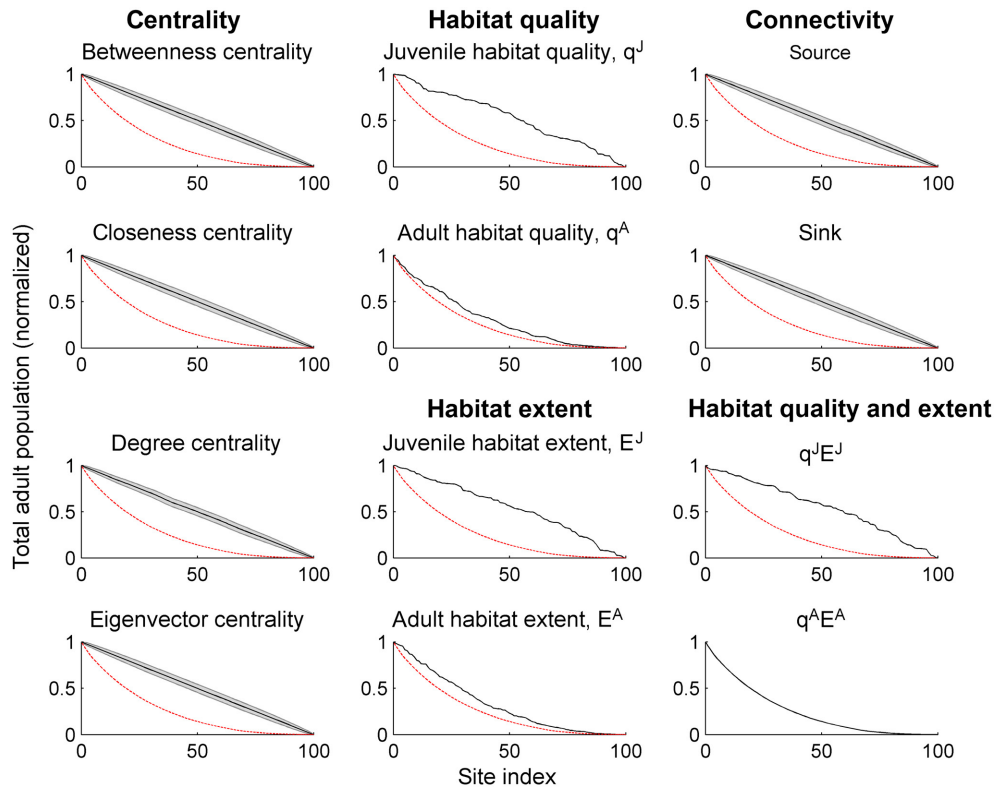


Fig. 2. Sequential deletion of nodes using 1000 Watts–Strogatz connectivity structures with parameters WS ( $n = 100$ ,  $K = 30$ ,  $\beta = 0.05$ ). Level of local larval retention is 10%,  $L = 100$ ,  $J_{\max} = 10^{20}$ , and  $A_{\max} = 10^5$ . The red dotted lines are the paths taken by the greedy algorithm, while the black lines are the results of different protection strategies. The result for  $q^A E^A$  overlaps the path taken by the greedy algorithm. Sites are indexed according to decreasing order of indicated metric (e.g., arranged in terms of decreasing function as source, sink).

true even under the extreme condition of 0% larval retention ( $l = 0$ ; Fig. 5d). The structure of the larval connectivity network also has no effect on the resulting protection strategy (Fig. 5e–f). The result is robust to all tested values of larval production per adult population,  $L$  (Appendix S1: Figs. S2–S4).

For Model 2, where larval output is a function of the successful connections and dependent on the adult population size, the results are the same as for Model 1. For  $J_{\max} > A_{\max}$ , the protection strategy based on preserving high adult habitat carrying capacity is optimal, whereas for  $A_{\max} > J_{\max}$ , a protection strategy based on preserving high juvenile habitat carrying capacity is optimal (Appendix S1: Figs. S9–S12, see also Figs. S13–S16 for the similar case where there is no adult carrying capacity). The results remain the same with and without self-seeding and are

robust to all tested values of larval production per adult,  $L$  (Appendix S1: Figs. S9–S12). These results are the same for the three network models considered in this study (Appendix S1: Tables S1–S3).

For Model 3, where larval production is a function only of successful connections and not of the adult or spawning population size, the results differ from models 1 and 2. When the population is sensitive to adult and juvenile habitats and there is a low but constant level of larval production per successful connection, a protection strategy based on connectivities is an optimal strategy for both Erdős–Rényi and Barabási–Albert networks (Appendix S1: Tables S1 and S2) while protection strategies based on connectivities and habitats are almost equal for Watts–Strogatz network ( $L_C = 1$  in Appendix S1: Figs. S17 and S19). At high, constant larval production per successful

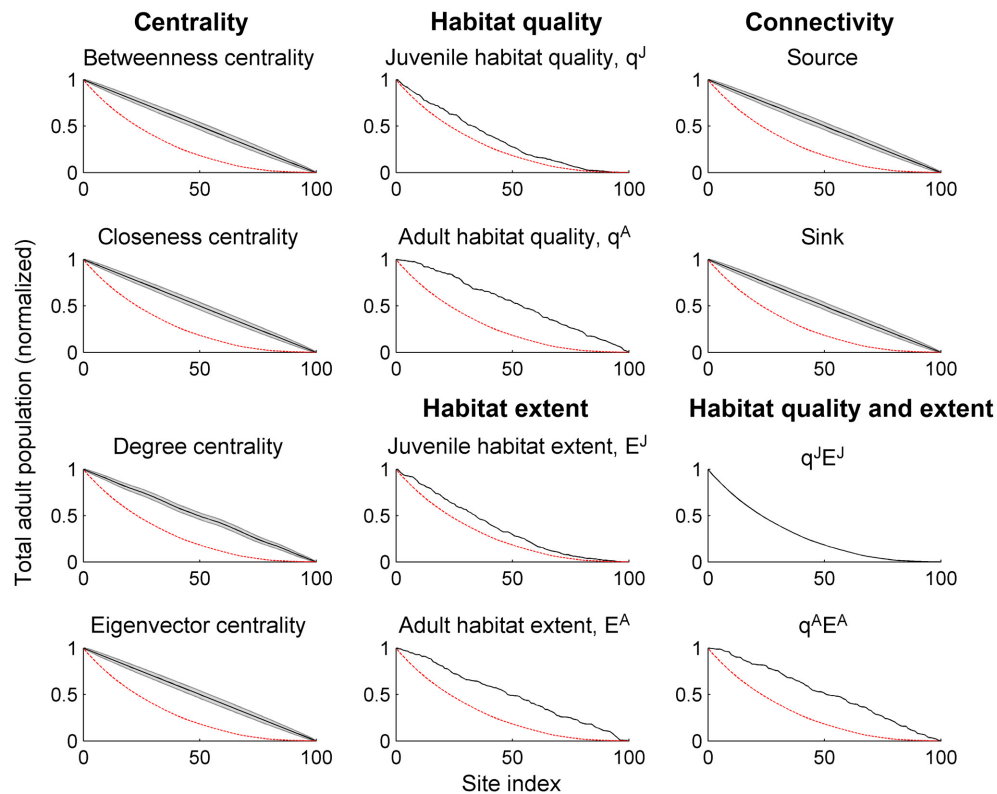


Fig. 3. Sequential deletion of nodes using 1000 Watts–Strogatz connectivity structures with parameters  $WS$  ( $n = 100, K = 30, \beta = 0.05$ ). Level of local larval retention is 10%,  $L = 100, J_{max} = 10^5$ , and  $A_{max} = 10^{20}$ . The red dotted lines are the paths taken by the greedy algorithm, while the black lines are the results of different protection strategies. The result for  $q^J E^J$  overlaps the path taken by the greedy algorithm. Sites are indexed according to decreasing order of indicated metric (e.g., arranged in terms of decreasing function as source, sink).

connection ( $L_C = 1000$  in Appendix S1: Figs. S18 and S20), a protection strategy based on preserving high habitat carrying capacities is optimal, similar to models 1 and 2, that is, for  $J_{max} > A_{max}$ , a protection strategy based on preserving high adult habitat carrying capacity is optimal while for  $A_{max} > J_{max}$ , a protection strategy based on preserving high juvenile habitat carrying capacity is optimal. If we remove the dependence of the adult population on habitat availability in Model 3, a protection strategy based on connectivities (sink, source, and node centralities) is optimal for the Erdős–Rényi and Barabási–Albert networks (Appendix S1: Tables S1 and S2), while for the Watts–Strogatz network, no persistent pattern is observed and protection strategies based on connectivities and habitat are almost the same in terms of performance (Appendix S1: Figs. S21–S24, Table S3).

## DISCUSSION AND IMPLICATIONS

We showed that for the metapopulation model of a population with a sessile adult stage and a dispersing larval stage, connectivity as the basis for prioritizing sites for protection becomes an optimal strategy only in limited situations with relatively extreme assumptions. Except in one biologically unreasonable case, habitat characteristics should dominate prioritization strategies. A site may have high connectivity, but the protection of such a site will not necessarily exert a high impact on the entire population, especially if the site has a low spawning population and low carrying capacity. Connectivity may be high, but the amount of transported larvae and their survivorship may be low.

Information on the point on the nursery–reef habitat continuum that limits the adult population



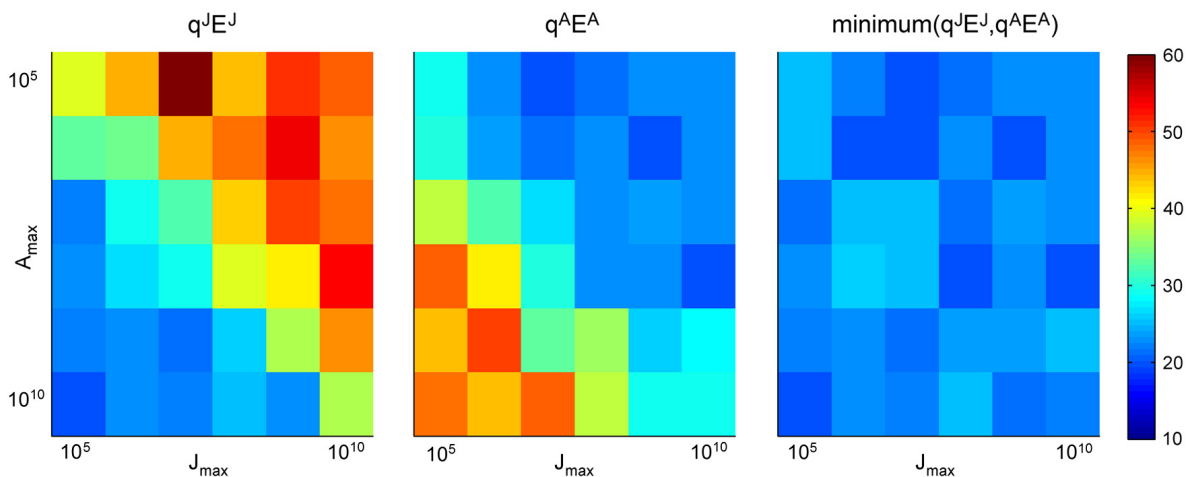


Fig. 4.  $C^{0.5}$  for different values of  $J_{\max}$  and  $A_{\max}$  using protection strategies based on (a) juvenile habitat carrying capacity ( $q^JE^J$ ), (b) adult habitat carrying capacity ( $q^AE^A$ ), and (c) minimum value of juvenile and adult habitat carrying capacities, that is, minimum ( $q^JE^J$ ,  $q^AE^A$ ). Lower values of  $C^{0.5}$  indicate that the strategy is more efficient in identifying key sites for protection.

is crucial in designing strategies for protection. If the juvenile habitat limits the adult population of the metapopulation, juvenile habitat's carrying capacity (extent and quality) should be the basis for protection. If the adult habitat limits the adult population, the quality and extent of the adult habitat should serve as the basis for protection.

It has been argued that connectivity is easier to measure than habitat quality and that networks based on connectivity can be cost efficient (Berglund et al. 2012). We counter that this may rarely be the case, as measuring connectivity is difficult, while measuring habitat quality and extent is resource-intensive, but not difficult. In marine populations, the connectivity structure may be inferred from oceanographic models; however, verification of these structures, usually through genetic/DNA parentage analysis (e.g., Planes et al. 2009, Christie et al. 2010), may be costly. In a coral reef system, where many of the fish species have restricted home ranges, MPA managers regularly collect information on habitat quality and productivity (e.g., live hard coral cover, fish biomass) as part of their monitoring and evaluation mechanisms, thereby providing information that is directly available for a rapid evaluation of sites for protection.

We use the metric of total adult fish population to compare the performances of different protection strategies. There are other protection

goals, such as ensuring population persistence in a metapopulation (e.g., Hastings and Botsford 2006, Isaak et al. 2007), that need to be explored. Nonetheless, conservation gains can be maximized by protecting subpopulations with high carrying capacities that have been historically overfished (Gaines et al. 2010). By rebuilding degraded habitat in areas that previously had relatively high carrying capacities, the health of the whole metapopulation could be improved, as demonstrated by the case of scallop management in Georges Bank. The management of scallops on Georges Bank in the northeastern United States provides an excellent example of a species with a pelagic larval and sessile adult phase. Rotational management was used to close fishing in formerly productive areas to help rebuild habitat and biomass, which eventually led to a strong increase in both biomass and fishery yields (Repetto 2001). MPAs are typically enacted as fisheries management tools (i.e., to enhance catches or mitigate fishery impacts), and closing down the largest and most productive habitats may generate strong resistance from the stakeholders. An alternative, which has been deployed in the Georges Bank scallop fishery, is to focus on rebuilding once-prominent populations or to enact rotational closures that close down the areas with the largest carrying capacity in succession over a period of a few years or

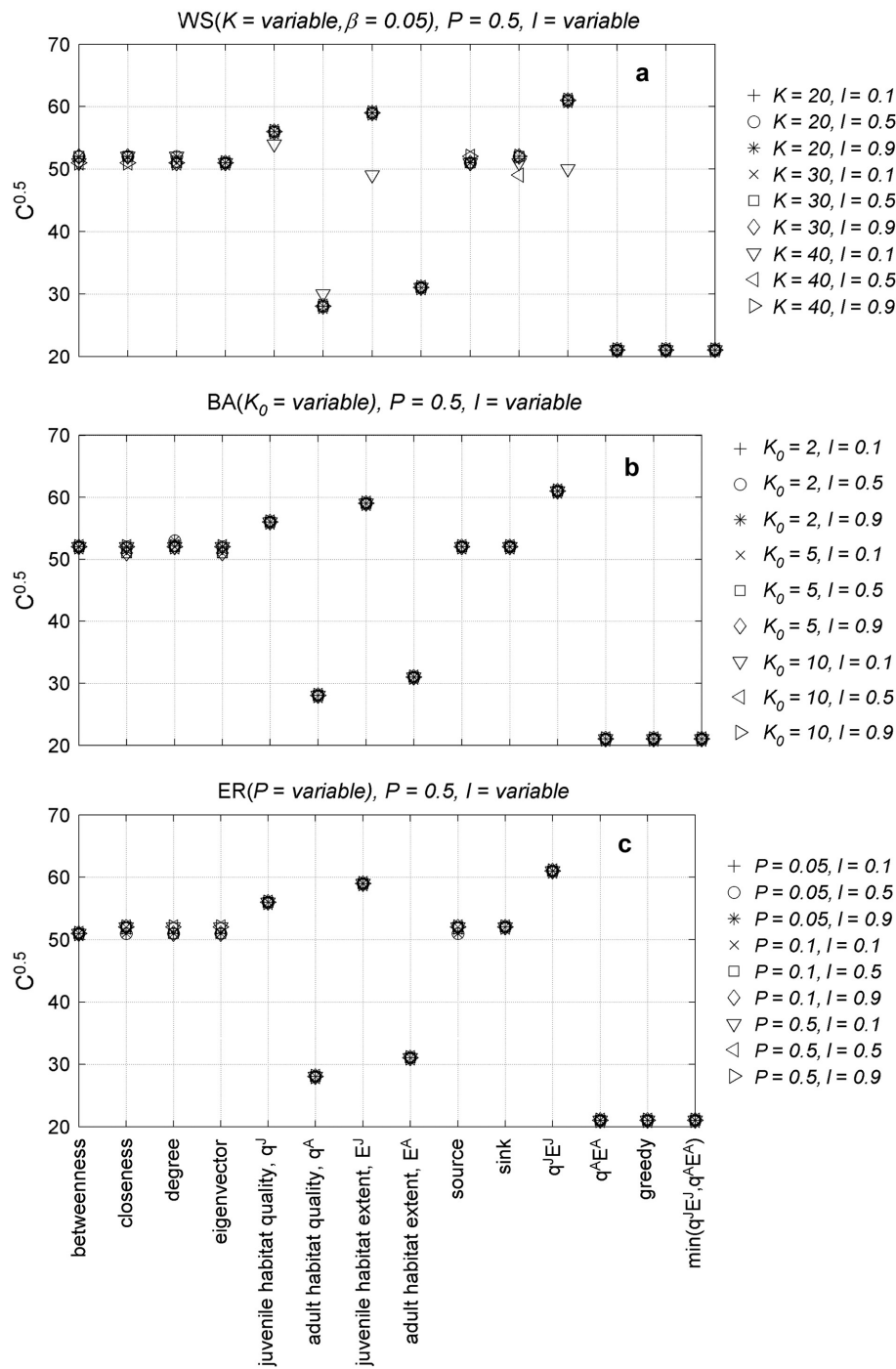


Fig. 5. Sensitivity of the model to different network structures and levels of larval retention for  $L = 100$ ,  $J_{\max} = 10^{20}$ , and  $A_{\max} = 10^5$ : (a) Watts–Strogatz model for variable network structure parameter  $K$  and larval retention  $l$ , (b) Barabási–Albert model for variable network structure parameter  $K$  and larval retention  $l$ , (c) Erdős–Rényi model for variable network structure parameter  $K$  and larval retention  $l$ , (d) variable network structure with zero larval retention, (e) Watts–Strogatz model for variable network structure parameter  $K$  and larval retention  $l$ , with  $P = 0$ , and (f) Watts–Strogatz model for variable network structure parameter  $K$  and larval retention  $l$ , with  $P = 1$ . A lower value of  $C^{0.5}$  indicates that the strategy is more efficient in identifying key sites for protection.

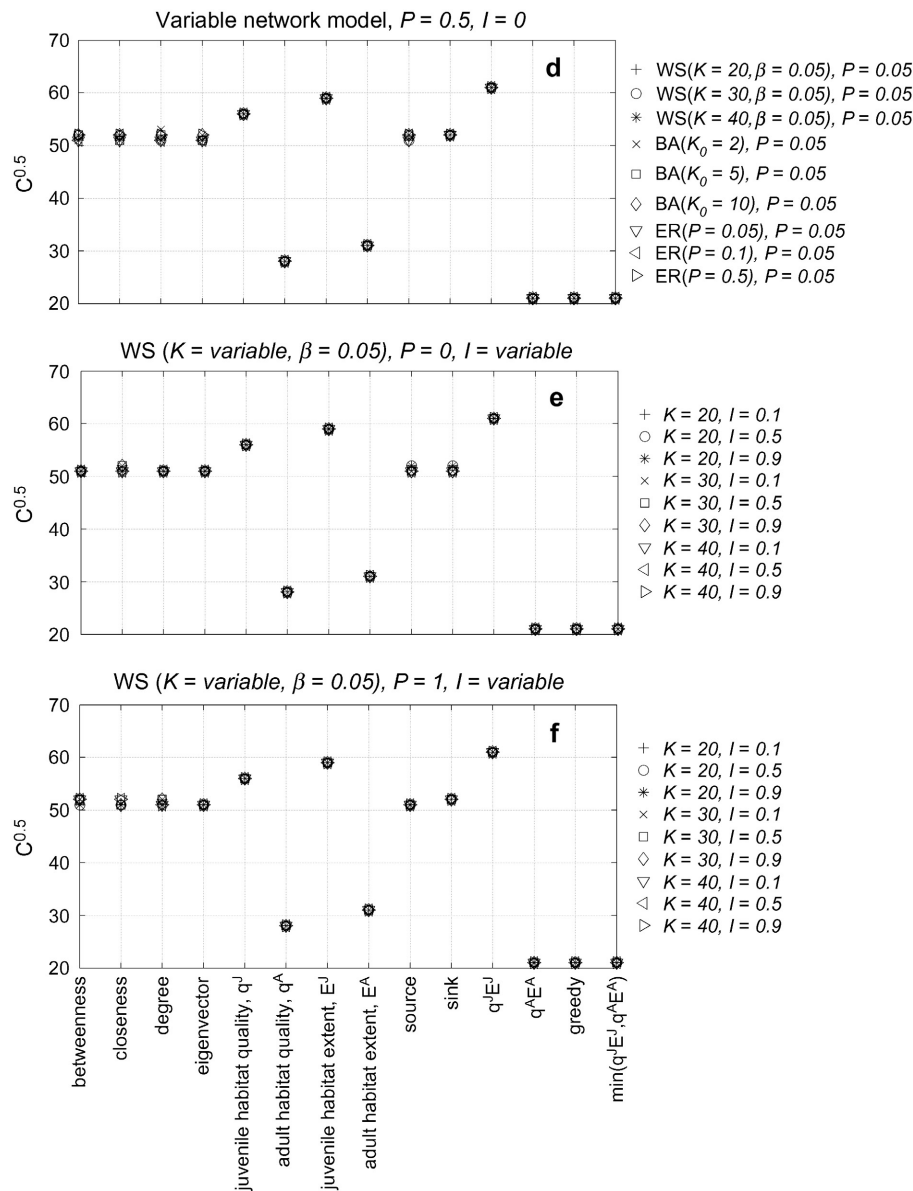


Fig. 5. Continued.

decades (i.e., close down the largest area for few years, open it for regulated harvesting, and then close down the second largest).

There are alternative ways to use rich analytic methods that can project the benefits of alternative reserve designs in a particular setting. In the data-rich context of California, detailed knowledge of oceanography, biology, and fisheries informed the design of a large network of protected areas (e.g., Kaplan et al. 2009, Watson et al. 2011, Rassweiler et al. 2012, White et al. 2013, Cabral et al. 2016).

However, for the vast majority of the ocean, such data and scientific insight do not currently exist and may never be readily available. As a result, approaches and insights that can help us decide how to achieve good conservation outcomes in the face of enormous uncertainty are valuable. Our findings suggest that the most important thing to focus on in the absence of more precise information is the quality and extent of habitats, which are the metrics for which it is easiest to obtain data. These methods and metrics are

probably more practical and useful (in the context of data-limited situation) than the highly successful approaches used in California.

Despite the strengths of our approach, there may be limitations to our findings when applied to real-world situations with limited data (similar to other studies that suggest MPA siting based on connectivity). While satellite data sets may be used to identify the extent of coral reef and mangrove patches and their proximity to each other (e.g., Cabral et al. 2015), measuring meaningful metrics of habitat quality for both of these ecosystems requires an intensive investment of resources. Typically, managers assess habitat quality using metrics including live coral cover, mangrove density, and habitat rugosity, but other reef and mangrove attributes that enhance fish populations should be identified and quantified. Furthermore, while small patches of reefs may be assumed to be a subpopulation, large reef patches may contain several subpopulations: Information on delineating subpopulations or habitat extents is needed.

Our model is similar to MacCall's (1990) Basin model, in which he used a spatially defined logistic model with varying carrying capacities across the model domain to examine how fish movement and distribution were related to habitat quality. Although our model explored dynamics of a population with a sessile adult stage, it is straightforward to extend our model to different levels of adult exchange, or "viscosity," in the terminology of the Basin model. As in the Basin model, good quality habitat supports greater fish biomass and productivity. The Basin model considers larval supply as a single distribution and does not explicitly identify the contribution of each habitat patch to larval production. The network approach used here explicitly models the larval production per subpopulation; the degradation of a subpopulation will have a direct impact on the larval supply to the connected subpopulations and thus an indirect impact on the entire metapopulation. Both our model and the Basin model use a logistic model to describe population dynamics, as is the case in many population models. The results should remain the same for a diverse set of sigmoidal population models and stock–recruitment relationships (Murray 2007).

Fisheries management has not adequately considered connectivity issues and often treats the

fishery as a single population. The modeling done here focused more on conservation measures, particularly on MPA network design in a context in which other sites are poorly managed. The role of habitats and connectivity in the context of fisheries should be explored in the future.

MPA networks are currently designed on the basis of habitat conditions (Gaines et al. 2010), making the implementation of the site-prioritization mechanism suggested here straightforward. Habitat restoration efforts, particularly in degraded habitats that were previously productive, are also justified, as our result shows that they will have a positive impact on the entire metapopulation. As a rule of thumb, managers should preserve high-quality and extensive habitat, and connectivity may be taken as given. This rule is robust to a diverse set of larval pathways tested here, given a high degree of connectivity between reef sites as elucidated in oceanographic (Roberts 1997, Melbourne-Thomas et al. 2011, Hogan et al. 2012) and molecular (Jones et al. 2005, Planes et al. 2009, Almany et al. 2013) connectivity studies. In terms of management, policies should prioritize the mitigation of stressors that are relevant to the degradation of habitat quality.

In non-selective, multispecies coral reef fisheries, connectivity varies for different species and even for closely related species (e.g., Becker et al. 2007), thereby adding to the difficulty of managing fisheries on the basis of connectivity. The current practice of siting MPAs is often based on habitat quality and extent; we expect that conservation, and potentially fisheries, benefits will occur as ecologically important sites are protected.

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## LITERATURE CITED

- Almany, G. R., M. L. Berumen, S. R. Thorrold, S. Planes, and G. P. Jones. 2007. Local replenishment of coral reef fish populations in a marine reserve. *Science* 316:742–744.
- Almany, G. R., et al. 2013. Dispersal of grouper larvae drives local resource sharing in a coral reef fishery. *Current Biology* 23:626–630.

- Barabási, A. L., and R. Albert. 1999. Emergence of scaling in random networks. *Science* 286:509–512.
- Becker, B. J., L. A. Levin, F. J. Fodrie, and P. A. McMillan. 2007. Complex larval connectivity patterns among marine invertebrate populations. *Proceedings of the National Academy of Sciences USA* 104:3267–3272.
- Berglund, M., M. Nilsson Jacobi, and P. R. Jonsson. 2012. Optimal selection of marine protected areas based on connectivity and habitat quality. *Ecological Modelling* 240:105–112.
- Bode, M., K. Burrage, and H. P. Possingham. 2008. Using complex network metrics to predict the persistence of metapopulation with asymmetric connectivity patterns. *Ecological Modelling* 214:201–209.
- Botsford, L. W., J. W. White, M. A. Coffroth, C. B. Paris, S. Planes, T. L. Shearer, S. R. Thorrold, and G. P. Jones. 2009. Connectivity and resilience of coral reef metapopulations in marine protected areas: matching empirical efforts to predictive needs. *Coral Reefs* 28:327–337.
- Cabral, R. B., S. D. Gaines, B. Johnson, T. W. Bell, and C. White. 2016. Drivers of redistribution of fishing and non-fishing effort after the implementation of a marine protected area network. *Ecological Applications*. <http://dx.doi.org/10.1002/eap.1446>
- Cabral, R. B., S. S. Mamauag, and P. M. Aliño. 2015. Designing a marine protected areas network in a data-limited situation. *Marine Policy* 59:64–76.
- Carson, H. S., G. S. Cook, P. C. López-Duarte, and L. A. Levin. 2011. Evaluating the importance of demographic connectivity in a marine metapopulation. *Ecology* 92:1972–1984.
- Christie, M. R., B. N. Tissot, M. A. Albins, J. P. Beets, Y. Jia, D. M. Ortiz, S. E. Thompson, and M. A. Hixon. 2010. Larval connectivity in an effective network of marine protected areas. *PLoS ONE* 5:e15715.
- Cowen, R. K., and S. Sponaugle. 2009. Larval dispersal and marine population connectivity. *Annual Review of Marine Science* 1:443–466.
- Crowder, L. B., S. J. Lyman, W. F. Figueira, and J. Priddy. 2000. Source-sink population dynamics and the problem of siting marine reserves. *Bulletin of Marine Science* 66:799–820.
- Doherty, P. J., and T. Fowler. 1994. An empirical test of recruitment limitation in a coral reef fish. *Science* 263:935–939.
- Eggleston, D. B. 1995. Recruitment in Nassau grouper *Epinephelus striatus*: post-settlement abundance, microhabitat features, and ontogenetic habitat shifts. *Marine Ecology Progress Series* 124:9–22.
- Erdős, P., and A. Rényi. 1960. On the evolution of random graphs. *Publications of the Mathematical Institute of the Hungarian Academy of Sciences* 5:17–61.
- Figueira, W. F. 2009. Connectivity or demography: defining sources and sinks in coral reef fish metapopulations. *Ecological Modelling* 220:1126–1137.
- Figueira, W. F., and L. B. Crowder. 2006. Defining patch contribution in source-sink metapopulations: the importance of including dispersal and its relevance to marine systems. *Population Ecology* 48:215–224.
- Fleishman, E., C. Ray, P. Sjögren-Gulve, C. L. Boggs, and D. D. Murphy. 2002. Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. *Conservation Biology* 16:706–716.
- Gaines, S. D., B. Gaylord, and J. L. Largier. 2003. Avoiding current oversights in marine reserve design. *Ecological Applications* 13(sp1):32–46.
- Gaines, S. D., C. White, M. H. Carr, and S. R. Palumbi. 2010. Designing marine reserve networks for both conservation and fisheries management. *Proceedings of the National Academy of Sciences USA* 107:18286–18293.
- Gilmour, J. P., L. D. Smith, A. J. Heyward, A. H. Baird, and M. S. Pratchett. 2013. Recovery of an isolated coral reef system following severe disturbance. *Science* 340:69–71.
- Griffen, B. D., and J. M. Drake. 2008. Effects of habitat quality and size on extinction in experimental populations. *Proceedings of the Royal Society of London B: Biological Sciences* 275:2251–2256.
- Griffen, B. D., and A. P. Norelli. 2015. Spatially variable habitat quality contributes to within-population variation in reproductive success. *Ecology and Evolution* 5:1474–1483.
- Halpern, B. S., S. D. Gaines, and R. R. Warner. 2005. Habitat size, recruitment, and longevity as factors limiting population size in stage-structured species. *American Naturalist* 165:82–94.
- Hanski, I. 1998. Metapopulation dynamics. *Nature* 396:41–49.
- Hastings, A., and L. W. Botsford. 2006. Persistence of spatial populations depends on returning home. *Proceedings of the National Academy of Sciences USA* 103:6067–6072.
- Hogan, J. D., R. J. Thiessen, P. F. Sale, and D. D. Heath. 2012. Local retention, dispersal and fluctuating connectivity among populations of a coral reef fish. *Oecologia* 168:61–71.
- Isaak, D. J., R. F. Thurow, B. E. Rieman, and J. B. Dunham. 2007. Chinook salmon use of spawning patches: relative roles of habitat quality, size, and connectivity. *Ecological Applications* 17:352–364.
- Jaquière, J., J. Guélat, T. Broquet, L. Berset-Brandli, E. Pellegrini, R. Moresi, A. H. Hirzel, and N. Perrin. 2008. Habitat-quality effects on metapopulation dynamics in greater white-toothed shrews, *Crocidura russula*. *Ecology* 89:2777–2785.

- Jones, G. P., M. J. Milicich, M. J. Emslie, and C. Lunow. 1999. Self-recruitment in a coral reef fish population. *Nature* 402:802–804.
- Jones, G. P., S. Planes, and S. R. Thorrold. 2005. Coral reef fish larvae settle close to home. *Current Biology* 15:1314–1318.
- Jones, D. L., J. F. Walter, E. N. Brooks, and J. E. Serafy. 2010. Connectivity through ontogeny: fish population linkages among mangrove and coral reef habitats. *Marine Ecology Progress Series* 401: 245–258.
- Kaplan, D. M., L. W. Botsford, M. R. O'Farrell, S. D. Gaines, and S. Jorgensen. 2009. Model-based assessment of persistence in proposed marine protected area designs. *Ecological Applications* 19:433–448.
- 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.
- Kininmonth, S. J., G. De'ath, and H. P. Possingham. 2010. Graph theoretic topology of the Great but small Barrier Reef world. *Theoretical Ecology* 3: 75–88.
- Kinlan, B. P., and S. D. Gaines. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* 84:2007–2020.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15:237–240.
- Levins, R. 1970. Extinction. Pages 77–107 in M. Desternhaber, editor. *Some mathematical problems in biology*. American Mathematical Society, Providence, Rhode Island, USA.
- Lockwood, D. R., A. Hastings, and L. W. Botsford. 2002. The effects of dispersal patterns on marine reserves: Does the tail wag the dog? *Theoretical Population Biology* 61:297–309.
- López-Duarte, P. C., H. S. Carson, G. S. Cook, F. J. Fodrie, B. J. Becker, C. DiBacco, and L. A. Levin. 2012. What controls connectivity? An empirical, multi-species approach. *Integrative and Comparative Biology* 52:511–524.
- MacCall, A. D. 1990. *Dynamic geography of marine fish populations*. Washington Sea Grant Program, Seattle, Washington, USA, 153 pp.
- Mamaug, S. S. 2011. *Status of groupers (sub-family Epinephelae, family Serranidae) in the Philippines from their broad-scale and fine-scale distributions with emphasis on Epinephelus coioides*. A Doctoral Dissertation submitted to the Marine Science Institute, College of Science, University of the Philippines Diliman, Quezon City, Philippines, 207 pp.
- Man, A., R. Law, and N. V. Polunin. 1995. Role of marine reserves in recruitment to reef fisheries: a metapopulation model. *Biological Conservation* 71:197–204.
- McClanahan, T. R. 1994. Kenyan coral reef lagoon fish: effects of fishing, substrate complexity, and sea urchins. *Coral Reefs* 13:231–241.
- Melbourne-Thomas, J., C. R. Johnson, P. M. Aliño, R. C. Geronimo, C. L. Villanoy, and G. G. Gurney. 2011. A multi-scale biophysical model to inform regional management of coral reefs in the western Philippines and South China Sea. *Environmental Modelling & Software* 26:66–82.
- Mitarai, S., D. A. Siegel, and K. B. Winters. 2008. A numerical study of stochastic larval settlement in the California Current system. *Journal of Marine Systems* 69:295–309.
- Moilanen, A., and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. *Ecology* 79:2503–2515.
- Mumby, P. J., et al. 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* 427:533–536.
- Murray, J. D. 2007. *Mathematical biology: I. An introduction*. Third edition. Springer, New York, New York, USA.
- Nagelkerken, I., M. G. Grol, and P. J. Mumby. 2012. Effects of marine reserves versus nursery habitat availability on structure of reef fish communities. *PLoS ONE* 7:e36906.
- Nagelkerken, I., S. Kleijnen, T. Klop, R. A. C. J. Van Den Brand, E. C. de La Moriniere, and G. Van der Velde. 2001. Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. *Marine Ecology Progress Series* 214:225–235.
- Nagelkerken, I., C. M. Roberts, G. Van Der Velde, M. Dorenbosch, M. C. Van Riel, E. C. De La Moriniere, and P. H. Nienhuis. 2002. How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale. *Marine Ecology Progress Series* 244:299–305.
- Neudecker, S. 1982. *Ecological relationships of chaetodontid and pomacanthid fishes at St. Croix*. Doctoral dissertation. University of California, Davis, Davis, California, USA.
- Planes, S., G. P. Jones, and S. R. Thorrold. 2009. Larval dispersal connects fish populations in a network of marine protected areas. *Proceedings of the National Academy of Sciences USA* 106:5693–5697.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- Rassweiler, A., C. Costello, and D. A. Siegel. 2012. Marine protected areas and the value of spatially optimized

- fishery management. *Proceedings of the National Academy of Sciences USA* 109:11884–11889.
- Repetto, R. 2001. A natural experiment in fisheries management. *Marine Policy* 25:251–264.
- Rijnsdorp, A. D., F. A. Van Beek, S. Flatman, R. M. Millner, J. D. Riley, M. Giret, and R. De Clerck. 1992. Recruitment of sole stocks, *Solea solea* (L.), in the Northeast Atlantic. *Netherlands Journal of Sea Research* 29:173–192.
- Roberts, C. M. 1997. Connectivity and management of Caribbean coral reefs. *Science* 278:1454–1457.
- Roberts, C. M., and R. F. G. Ormond. 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Marine Ecology Progress Series* 41:1–8.
- Rodwell, L. D., E. B. Barbier, C. M. Roberts, and T. R. McClanahan. 2003. The importance of habitat quality for marine reserve fishery linkages. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 171–181.
- Roughgarden, J., S. Gaines, and H. Possingham. 1988. Recruitment dynamics in complex life cycles. *Science* 241:1460–1466.
- Sale, P. F. 2002. The science we need to develop for more effective management. Pages 361–376 in P. F. Sale, editor. *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, San Diego, California, USA.
- Sale, P. F., I. Hanski, and J. P. Kritzer. 2006. The merging of metapopulation theory and marine ecology: establishing the historical context. Pages 9–28 in P. F. Sale and J. P. Kritzer, editors. *Marine metapopulations*. Elsevier Academic Press, San Diego, California, USA.
- Shima, J. S., and C. W. Osenberg. 2003. Cryptic density dependence: effects of covariation between density and site quality in reef fish. *Ecology* 84:46–52.
- Siegel, D. A., S. Mitarai, C. J. Costello, S. D. Gaines, B. E. Kendall, R. R. Warner, and K. B. Winters. 2008. The stochastic nature of larval connectivity among nearshore marine populations. *Proceedings of the National Academy of Sciences USA* 105:8974–8979.
- Thomas, J. A., N. A. Bourn, R. T. Clarke, K. E. Stewart, D. J. Simcox, G. S. Pearman, R. Curtis, and B. Goodger. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society of London B: Biological Sciences* 268:1791–1796.
- Tupper, M., and R. G. Boutilier. 1997. Effects of habitat on settlement, growth, predation risk and survival of a temperate reef fish. *Marine Ecology Progress Series* 151:225–236.
- Urban, D., and T. Keitt. 2001. Landscape connectivity: a graph-theoretic perspective. *Ecology* 82:1205–1218.
- Verweij, M. C., I. Nagelkerken, I. Hans, S. M. Ruseler, and P. R. Mason. 2008. Seagrass nurseries contribute to coral reef fish populations. *Limnology and Oceanography* 53:1540–1547.
- Visconti, P., and C. Elkin. 2009. Using connectivity metrics in conservation planning – When does habitat quality matter? *Diversity and Distributions* 15:602–612.
- Watson, J. R., D. A. Siegel, B. E. Kendall, S. Mitarai, A. Rassweiler, and S. D. Gaines. 2011. Identifying critical regions in small-world marine metapopulations. *Proceedings of the National Academy of Sciences USA* 108:E907–E913.
- Watts, D. J., and S. H. Strogatz. 1998. Collective dynamics of ‘small-world’ networks. *Nature* 393:409–410.
- White, J. W., et al. 2013. A comparison of approaches used for economic analysis in marine protected area network planning in California. *Ocean & Coastal Management* 74:77–89.
- Wilson, S. K., S. C. Burgess, A. J. Cheal, M. Emslie, R. Fisher, I. Miller, N. V. Polunin, and H. Sweatman. 2008. Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. *Journal of Animal Ecology* 77: 220–228.
- Wynne, S. P., and I. M. Côté. 2007. Effects of habitat quality and fishing on Caribbean spotted spiny lobster populations. *Journal of Applied Ecology* 44:488–494.

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