Catastrophes, connectivity, and Allee effects in the design of marine reserve networks

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Abstract

Catastrophic events, like oil spills and hurricanes, occur in many marine systems. These events, although rare, can still have disproportionately large effects on population dynamics. One management strategy to buffer against catastrophes is the establishment of a marine reserve network. In a network, an individual reserve can be recolonized after a disturbance event by organisms from an unaffected reserve—acting as an insurance policy. Management choices about the size and spacing of reserves ultimately determines their success or failure. We use a set of simple models to examine how organism life-history and the disturbance regime interact to determine the optimal reserve spacing. Our results show that the optimal spacing between reserves increases when accounting for catastrophes. This result is accentuated when Allee effects interact with catastrophes to increase the probability of extinction. We also show that classic tradeoffs between conservation and fishing objectives disappear in the presence of catastrophes.

Key words: catastrophes, disturbance, marine protected area, marine reserves, rare events, reserve network

1 Introduction

Marine protected areas (MPAs), including no-take marine reserves (Lubchenco et al. 2003), are increasingly being used as a form of ecosystem-based management (Wood et al. 2008). Desired outcomes of MPAs include increases in biomass and population size

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as well as spillover to harvested areas (Lester et al. 2009; Gaines et al. 2010; Baskett and Barnett 2015). Beyond individual reserves, networks of reserves can connect over larger areas given the long-distance passive dispersal of many marine organisms at early life history stages (Kinlan and Gaines 2003). Even in situations where each single reserve is not self-sustaining, network persistence can still be possible (Hastings and Botsford 2006). This overall network persistence depends on the specific size of reserves and the spacing between them (Botsford et al. 2001; 2003; Gerber et al. 2003; Gaines et al. 2010).

The outcome and optimal design of reserve networks can depend on environmental variability, including disturbances (Halpern et al. 2006; Cabral et al. 2017b; Aalto et al. 2019). Marine systems are inherently variable due to seasonal forces affecting temperature and upwelling, disturbances, and longer term cycles including El Niño (Fiedler 2002; Doney et al. 2012; White and Hastings 2018). Several of these factors (e.g. marine heat waves) are expected to become stronger or more variable in the future because of climate change (Oliver et al. 2018). This variability inevitably affects the population dynamics and distributions of many organisms. In addition, environmental variability or uncertainty can alter the optimal management strategies (Halpern et al. 2006). For example, temporal variability can increase the role of marine reserves in increasing population persistence (Mangel 2000). Game et al. (2008b) show that the level of environmental variability, in particular cyclones, alters the optimal placement of marine reserves to enhance coral reef persistence.

As an extreme form of environmental variability, disturbances (i.e. rare events or catastrophes) in marine systems can include bleaching events, hurricanes, oil spills, hypoxia, and disease outbreaks (Mangel and Tier 1994; Allison et al. 2003; Game et al. 2008b;a; Aalto et al. 2019). Given disturbances, the individual reserves within a network can act as an insurance policy for other reserves—a portfolio effect across reserves (Wagner et al. 2007). Disturbances can increase the amount of protection needed to achieve reserve goals (Allison et al. 2003) and increase the optimal distance between reserves (Wagner et al. 2007). Reserves placed too close together will potentially be affected by the same disturbance event simultaneously, preventing post-disturbance resettlement. Conversly, reserves placed too far apart also reduce the probability of successful dispersal between protected areas. Thus, when incorporating catastrophes into reserve network design, spatial scales of species movement and disturbance become important (Quinn and Hastings 1987; Wagner et al. 2007; Blowes and Connolly 2012) and can alter the optimal size and spacing of reserves within a network.

Disturbances can have particularly strong effects in systems that exhibit alternative stable states (Paine et al. 1998; Fabina et al. 2015; Dennis et al. 2016) by shifting a system from one state to another (Scheffer et al. 2001; Scheffer and Carpenter 2003). When a system moves from one state to another, hysteresis can act to make it more difficult to move back to the original state. In spatial systems with alternative stables states, a population that has shifted to an unfavorable state (e.g. local extinction) can be rescued by immigrants from another location. Strong Allee effects, or positive density-dependence at low densities, are one source of alternative stable states in ecological systems (Dennis et al. 2016). Allee effects have been well-documented for a number of species, including marine fishes (Hutchings 2013). Species that experience Allee effects and disturbances

have a higher extinction risk (Dennis et al. 2016; Aalto et al. 2019).

We build a series of models to quantify the optimal distances between reserves affected by disturbances. We first consider a set of simple population models of two-patch systems. This is analogous to Wagner et al. (2007), but with the added realism of density-dependent recruitment which can be an important buffer against environmental variability (Botsford et al. 2015). We then extend this framework to investigate how Allee effects and dispersal ability interact with the disturbance regime characteristics (e.g. frequency and magnitude) to affect the optimal spacing between reserves. This builds on work by Aalto et al. (2019) as they focused on global, as opposed to local, disturbances and they did not study spacing questions. Finally, we examine a spatially-explicit, multiple patch model of a coastline to explore the robustness of conclusions from the two-patch scenario and the role of fishing on network design.

2 Methods and models

2.1 Two-patch model

First, we use a two-patch, coupled Beverton-Holt model. In patch i, N_i is the population size. During each time step, we model three sequential events: 1) production (reproduction and growth), 2) dispersal, and 3) disturbance (Figure 1). We incorporate density-dependence in production with a Beverton-Holt function, G_i, where $r_i(t)$ is the growth rate and K_i is the carrying capacity (Figure S1). We describe r_i as a normal distribution to allow temporal variability in the growth rate. We assume both patches are reserves where no fishing occurs. This implicitly contains a "scorched earth" assumption that fishing removes all biomass outside of these two patches (Botsford et al. 2001).

Density-dependence factors into production in two ways. First, the denominator of equation 1 allows for negative density-dependence as N increases. Second, as we increase ω, the relationship between $N(t)$ and $N(t+1)$ at low $N(t)$ goes from concave to convex. Biologically, this means that when $\omega > 1$ there is an Allee effect present (i.e. positive density-dependence),

$$\begin{aligned} G_1 &= \tfrac{r_1(t)N_1(t)^\omega}{1+N_1(t)^\omega/K_1} \\ G_2 &= \tfrac{r_2(t)N_2(t)^\omega}{1+N_2(t)^\omega/K_2}. \end{aligned} \tag{1}$$

We connect the two patches via the dispersal, with fraction ϵ of dispersing individuals (Figure 1b). Similar to a typical dispersal kernel, we model dispersal success as an exponentially decaying function of distance, d, between reserves at a rate δ to yield the post-dispersal population sizes:

$$\begin{aligned} N_1'(t) &= (1-\epsilon)G_1 + \epsilon e^{-\delta d} G_2 \\ N_2'(t) &= (1-\epsilon)G_2 + \epsilon e^{-\delta d} G_1. \end{aligned} \tag{2}$$

We also include disturbance in the model. We assume disturbance occurs after growth and dispersal. Disturbance on a patch, M_i, is given by a binomial distribution with probability, p_i. If a patch is affected by a disturbance, the other patch has a probability $e^{-\gamma d}$

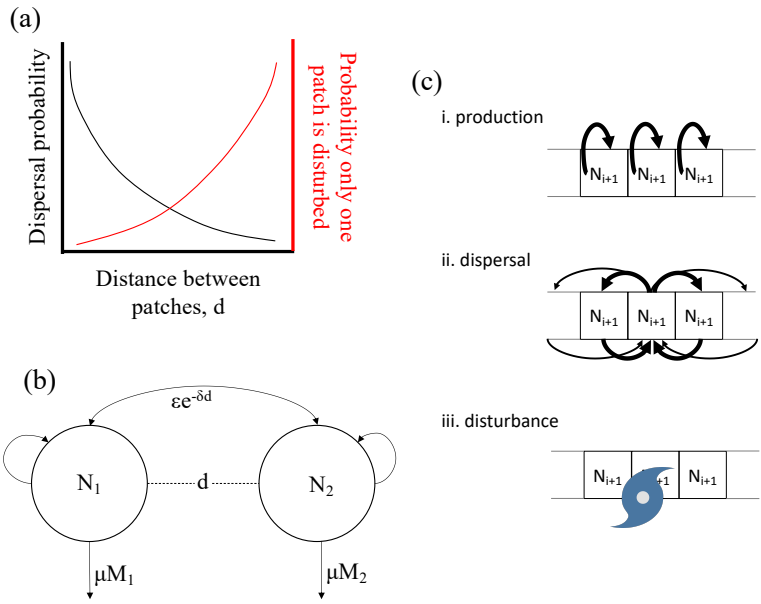

FIGURE 1: (a) Conceptual trade-off between successful dispersal probability and probability that disturbance only affects a single patch locally for different distances between patches, d. (b) Model diagram for the two-patch reserve scenario. Here N_i is the abundance in patch i, μM_1 is the mortality caused by disturbance, and $\epsilon e^{-\delta d}$ is the probability of successful dispersal. The arrows pointing out and back towards the same patch denote the recruitment process. (c) Model for n-patches with dispersal between patches (denoted by arrows connecting patches), recruitment within patches (given by the self-arrow), and a disturbance affecting a patch in the middle of the study area.

of also being affected by the disturbance, where γ is a shape parameter.

$$M_i(t) \sim \text{Binomial}(p_i) \tag{3}$$

$$M_j(t) \sim \text{Binomial}(e^{-\gamma d}) \tag{4}$$

A disturbance causes density-independent mortality, μ, for the entire patch. This mortality and $N_i'(t)$ give the number of individuals the following year:

$$\begin{aligned} N_1(t+1) &= (1-\mu M_1(t))N_1'(t) \\ N_2(t+1) &= (1-\mu M_2(t))N_2'(t). \end{aligned} \tag{5}$$

This then presents a trade-off in reducing patch distance to increase colonization potential, but increasing patch distance to reduce the probability of disturbance in both patches simultaneously (Figure 1a).

2.2 n-patch model

We extend our two-patch example to a model with n patches. The production function is the same as above, but we describe dispersal as a kernel. We describe this n-patch completely in the supplementary material.

2.3 Reserve network optimization

We examined three different management goals for determining the optimal reserve configuration: (1) maximize the probability of population persistence, measured as the amount of time above a certain population level, (2) maximize population biomass, and (3) maximize the amount of spillover for fisheries. For each management goal we systematically examine all possible reserve networks. This is possible when the number of patches is small. We limit the fraction of area that can be placed in reserves, specifically 20% of the patches (we test this assumption in Figure S4). For each simulation, after a burn in of 10 years, we record persistence, population biomass, and total catch. For each network, we run 100 simulations to account for stochasticity in model runs generated by the random disturbance locations and frequencies. We then find the mean value of these simulations to determine the success of that reserve network for each particular management goal. We examine the sensitivity of our results to changes in each of the parameters (Figures S2-S4).

Even with only 100 patches, there are 2^{100}, or 1.3 x 10^{30} possible reserve networks. Although not needed in this paper, for reserve networks with more patches, it would be necessary to use an evolutionary algorithm, or a related meta-heuristic optimization scheme (Chollett et al. 2017).

3 Results

In the two-patch model without an Allee effect, the population grows towards an equilibrium and is reduced in size by stochastic disturbance events (Figures 2a,b). Thus, catastrophes typically only affect the short-term transient dynamics, unless the disturbance were cause extinction of both patches. An Allee effect interacts with the disturbance regime to increase extinction risk because disturbances reduce the population below the Allee threshold (Figure 2d).

Without accounting for catastrophes (when disturbance frequency is zero), populations can only go extinct because of temporal variability in the growth rate. In this case, the optimal strategy to maximize population persistence is to place the reserves right next to each other (Figure 3). This strategy reduces the mortality rate during dispersal (Figures 4, S2, S3). Catastrophes then present a trade-off where reserves too close to one another can potentially both be affected by the same disturbance. To maximize population persistence, an some spacing between patches is optimal (Figure 3). However, as the disturbance frequency or magnitude increases, the population size (and population persistence) decreases. Thus, the optimal spacing between reserves increases only until the point at which the population goes extinct from the catastrophes (Figure 3). Allee

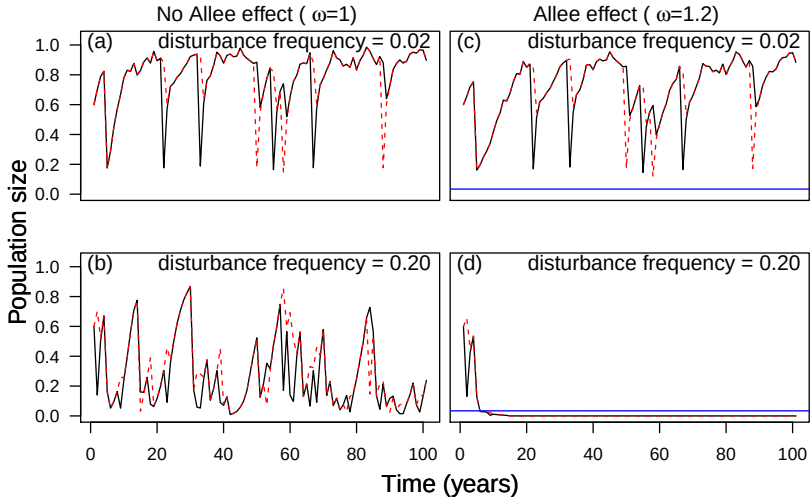

FIGURE 2: Example two-patch model simulation, each line denotes a different patch. The four panels represent different combinations of disturbance frequency and the presence ($\omega > 1$) or absence of an Allee effect. The horizontal line denotes the Allee threshold. The simulation is with the following model parameters: $r = 2.1$, $K = 1$, $\delta = 0.01$, $\epsilon = 0.5$, and distance between patches of 40.

effects interact with catastrophes to increase the optimal distances between patches as the disturbance frequency or magnitude increases (Figure 3).

In line with expectations, the optimal distance between reserves increases with higher probability of successful dispersal (Figures 4, S2). At low disturbance levels, dispersal is more important and consequently small inter-patches distances are optimal (Figure 4). Conversely, when disturbances are likely to occur in both patches simultaneously it is optimal to bring reserves closer together (Figure 4). This happens because disturbances are large enough to drive the entire reserve network to extinction and the best management strategy is to bring reserves closer.

3.1 n-patch simulation model

Our n-patch model without disturbances supports previous work that for a fixed fraction of a coastline in reserves, a single, large reserve maximizes population persistence (Botsford et al. 2001). With disturbances, the optimal spacing between reserves increases unless disturbances are too frequent (Figure 5). Compared to the persistence objective, to maximize biomass, it is always best to place reserves right next to each other, regardless of disturbance level (Figure 5). To maximize the fisheries yield from spillover, the optimal strategy is to spread out reserves unless disturbances become too frequent (Figure 5). Spreading out reserves increases the proportion of dispersers exposed to fishing outside reserves. With a moderate disturbance probability, the optimal spacing between reserves is nearly the same for the fishing and persistence objectives (Figure 5). As we increase the fraction of coastline protected, reserves can be placed closer together (Figure S4).

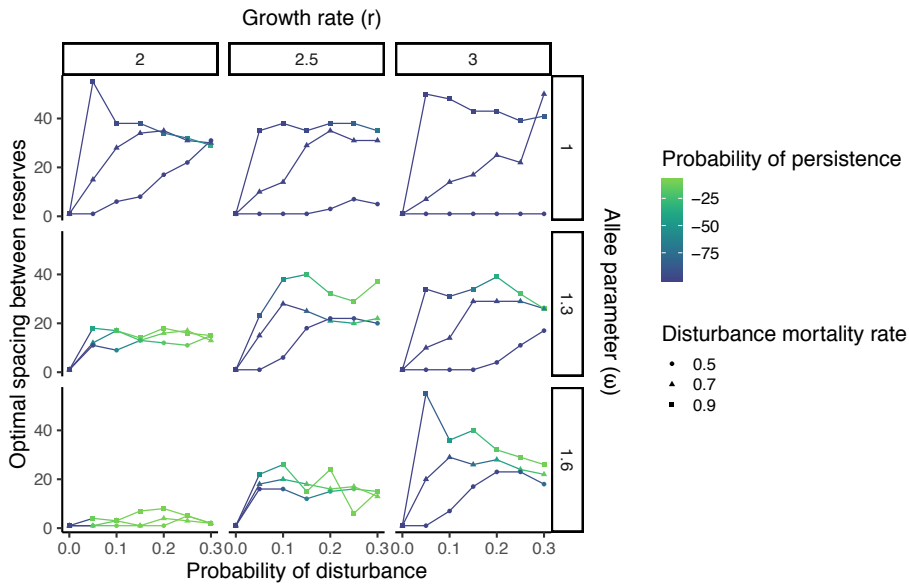

FIGURE 3: Optimal spacing for population persistence given different frequencies and magnitudes of disturbances. This is for the two-patch, Beverton-Holt model without (ω=1) and with an Allee effect (ω>1). These simulations are with the same parameter values as in Figure 2.

All of our above results include a "scorched earth" assumption—where there is 100% mortality for individuals outside of the reserves. When we relaxed this assumption, we found that, for reduced fishing pressure, persistence was maximized when reserves were placed close together at low disturbance frequencies (Figure 6). At high disturbance frequencies, this relationship reverses and reduced fishing pressure allows for reserves to be placed farther apart (Figure 6).

4 Discussion

Disturbances increase the spacing in reserve networks to achieve an objective of maximizing persistence (Figures 3,5). The increased distance decreased the probability that both reserves would be affected by the same disturbance. In a similar effort, Game et al. (2008b) used MARXAN to minimize the impact of coral bleaching in a reserve network of the Great Barrier Reef, Australia. They found that explicitly including disturbances a different optimal reserve design was found. However, their approach was static (i.e. did not include temporal dynamics) for simplicity, and did not consider more biological dynamics like connectivity or Allee effects.

We build on the work by Wagner et al. (2007) by adding density-dependence. When we included an Allee effect in our model, reserves had to be spread out to increase persistence (Figures 2d,3). A strong Allee effect creates alternative stable states with a tipping

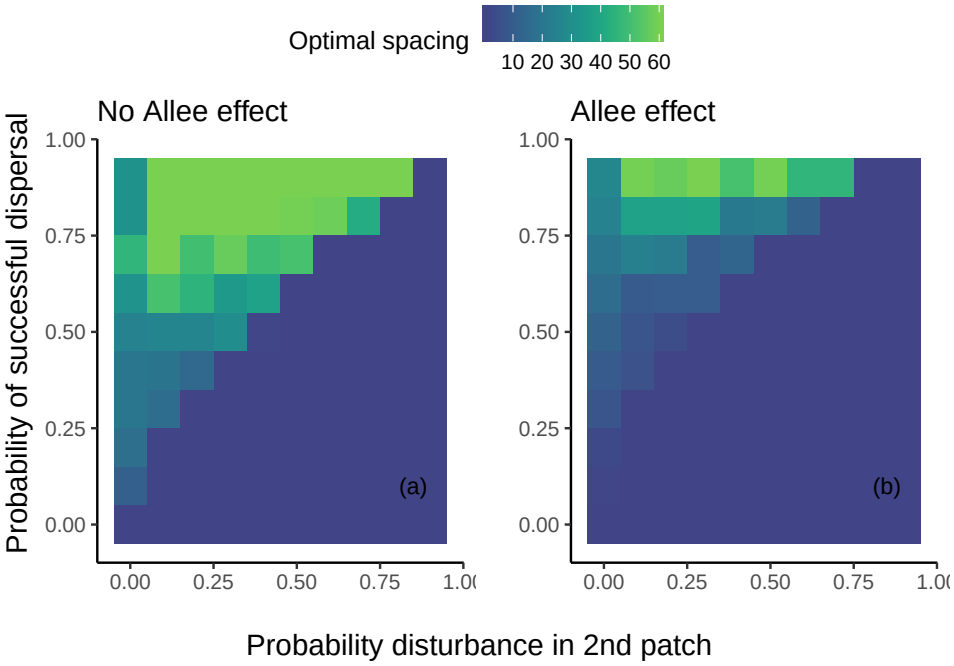

FIGURE 4: The optimal spacing between reserves for population persistence given different combinations of successful dispersal probability (to a patch 50 units away) and the probability that a disturbance in one patch affects the nearby second patch (at a distance of 50 units away). Simulations here are for a Beverton-Holt model (a) without and (b) with an Allee effect and the same paramter values as in figure 2.

point at the Allee threshold. Catastrophes interact with Allee effects by causing a regime shift to an alternative stable state (Dennis et al. 2016). Thus, it is necessary to spread out reserves farther in cases where Allee effects are present (Figure 3). This allows reserves to more effectively act as an insurance policy for one another. This will be particularly important for species like Atlantic cod (*Gadus morhua*) or Alaskan walleye pollock (*Theragra chalcogramma*) where Allee effects have been identified (Hutchings 2013). Aalto et al. (2019) studied a population of green abalone (*Haliotis fulgens*) in Baja California Sur, Mexico which experiences an Allee effect through recruitment failure at low population densities. They show that a reserve network can increase persistence for abalone when they are exposed to catastrophic events. Our work builds on this by focusing on the specific design of reserve networks.

There are many objectives with ecosystem-based management—in particular marine reserve networks (Lester et al. 2009; Gaines et al. 2010). Importantly, we found that at intermediate disturbance levels, the optimal spacing between reserves was the same for both maximizing fishing and maximizing persistence. This conflicts with previous theoretical work where large, single reserves maximize persistence and smaller, spread out reserves maximize fishing (Gaines et al. 2010). This conflict typically arises because spreading out reserves maximizes spillover from reserves to fished areas. However, in

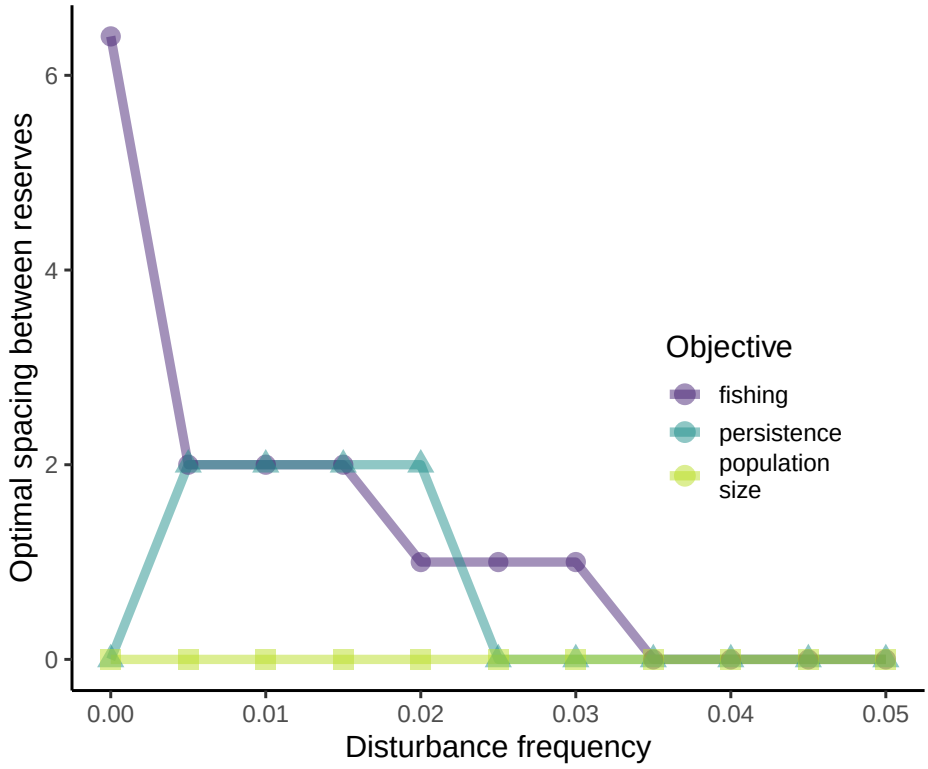

FIGURE 5: Optimal spacing between reserves (in an n-patch model) versus the probability of disturbance for three different objective functions. The parameter values used are: δ = 0.7, ω = 1.2, r = 3, and μ = 0.95.

our models, disturbances lead to a reserve design where reserves are spread out in order to decrease the probability of synchronous collapse of all reserve areas. This result is in line with previous work that examined environmental variability—but not catastrophes in particular—and marine reserves (Mangel 2000; Barnett et al. 2014).

In addition to the spacing between reserves, the management outside of reserves can also affect reserve network design. We found that decreasing fishing pressure outside reserves decreases the optimal spacing needed between reserves (Figure 6). This happens because of the reduced importance of disperser survival when fishing is reduced. Thus, spacing out reserves to avoid disturbances will be more effective in systems where "fishing the line" is less prevalent (Cabral et al. 2017a). McGilliard et al. (2011) also examined how catastrophic events and fishing pressure affect population persistence. In line with our work, they found that fishing management outside the reserves was important to ensure their success.

As with any model, we make a number of simplifications that would have to be modified if applying this model to a specific system. First, the patch connectivity would have to be determined using an approach like a regional oceanic modeling system (ROMS) model

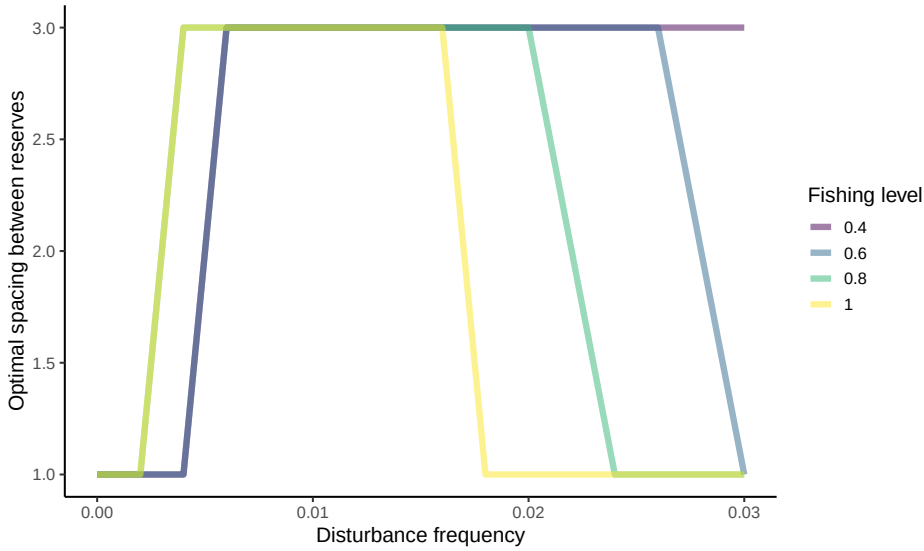

FIGURE 6: Optimal spacing between reserves (in an n-patch model) to maximize persistence for different disturbance frequencies and fishing levels outside of reserves (fraction of population harvested in each patch). The parameter values used here are: $\delta = 0.7$, $\omega = 1.2$, r = 3, and $\mu = 0.9$.

or other connectivity data (Shchepetkin and McWilliams 2005; Watson et al. 2012). We ignore age structure, which can have a buffering effect to disturbances if age classes are affected deferentially. To be useful in a real system, spatial and temporal data of disturbances are needed as disturbances can be spatially and temporally heterogeneous (Mellin et al. 2016). This heterogeneity affects the optimal placement of reserves if some parts of the coastline are less frequently disturbed than others. This may also include data on several disturbances that have different properties (e.g. coral bleaching versus hurricanes). Additionally, disturbances can be correlated in space and time, changing how they affect the system. For example, coral reefs that experience bleaching events too frequently may not have time to recover from the last bleaching event (Hughes et al. 2018). Lastly, our study focused on a single species. For multi-species systems, species can have different life histories (Baskett et al. 2007; White et al. 2015), including their dispersal abilities and susceptibility to disturbances. This can lead to scenarios where variable spacing between reserves is optimal.

This model has to be specified given system-specific life-history traits and disturbance regimes. Future plans include applying our approaches to a spatially-explicit model based on a specific study system. Our work can serve as a starting point for thinking about management and conservation strategies designed to be robust to future catastrophes.

5 Supporting Information

In the supporting material, we provide a description of the n-patch model, plots of the recruitment functions used, and additional figures. All code and data can be found at https://github.com/eastonwhite/MPA-disturbances

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