

Research

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

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Catastrophic events, like oil spills and hurricanes, occur in many marine systems. One potential role of marine reserves is buffering populations against disturbances, including the potential for disturbance-driven population collapses under Allee effects. This buffering capacity depends on reserves in a network providing rescue effects, setting up a tradeoff where reserves need to be connected to facilitate rescue, but also distributed in space to prevent simultaneous extinction. We use a set of population models to examine how dispersal ability and the disturbance regime interact to determine the optimal reserve spacing. We incorporate fishing in a spatially-explicit model to understand the effect of objective choice (e.g. conservation versus fisheries yield) on the optimal reserve spacing. We show that the optimal spacing between reserves increases when accounting for catastrophes with larger spacing needed 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. Specifically, we found that at intermediate levels of disturbance, it is optimal to spread out reserves in order to increase both population persistence and to maximize spillover into non-reserve areas.

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

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). Management goals of MPAs range from promoting sustainable fisheries to conserving biodiversity (Leslie 2005, Gaines et al. 2010). Potential outcomes of MPAs include increases in biomass and population size 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. 2017, Aalto et al. 2019). Marine systems are inherently dynamic due to seasonal forces affecting temperature and upwelling, disturbances and longer term cycles such as El Niño (Fiedler 2002, Doney et al. 2012, White and Hastings 2020). Several of these factors (e.g. storms, marine heat waves) are expected to become stronger or more variable in the future because of climate change (Bender et al. 2010, Oliver et al. 2018). This variability inevitably affects the population dynamics and distributions of many organisms. In addition, environmental fluctuations and uncertainty can alter the optimal management strategies (Halpern et al. 2006). For example, temporal variability in mortality can increase the role of marine reserves in population persistence (Mangel 2000). Further, the optimal reserve selection depends on the scale of stochasticity, either local demographic noise or regional disturbances, in the system (Quinn and Hastings 1987).

As an extreme form of environmental variability, disturbances (e.g. rare events or catastrophes) in marine systems can include marine heat waves, hurricanes, oil spills, hypoxia, economic shocks and disease outbreaks (Mangel and Tier 1994, Allison et al. 2003, Game et al. 2008a, Aalto et al. 2019, Cottrell et al. 2019, White et al. 2020a). Given disturbances, the individual reserves within a network can act as an insurance policy for other reserves, e.g. a portfolio effect across reserves (Pitchford et al. 2007, Wagner et al. 2007). The idea of a spatial insurance policy is one of the many arguments raised for allocating protection in more than one location in the ‘single large or several small’ (SLOSS) debate that originated in the terrestrial reserve literature (Fahrig 2013). For instance, Kallimanis et al. (2005) used a spatially-explicit metapopulation model to show that, while a single large area was favored with random disturbances, when disturbances were spatially autocorrelated this relationship no longer held. Similarly, with a more detailed and system-specific model, Helmstedt et al. (2014) showed that several, smaller predator exclusion patches were favored in the presence of catastrophes. However, findings from the terrestrial realm may not translate to the marine setting given the greater potential for passive dispersal, greater permeability of reserve boundaries and fishing rather than habitat loss as the primary anthropogenic impact (Carr et al. 2003, Halpern and Warner 2003).

For marine reserve networks, disturbances can increase the amount of protection needed to achieve management 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, reducing the likelihood that one reserve can maintain enough population to ‘rescue’ its neighbor (*sensu* Brown and Kodric-Brown 1977). Conversely, placing reserves too far apart minimizes the chance of successful dispersal. However, with certain forms of disturbances,

such as disease, population persistence might be increased by reducing dispersal (Sokolow et al. 2009, Kough et al. 2015). Thus, spatial scales of species movement and disturbance might alter the optimal size and spacing of reserves within a network (Quinn and Hastings 1987, Wagner et al. 2007, Blowes and Connolly 2012).

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). Specifically, if two states are locally stable under the same environmental conditions, hysteresis can occur, i.e. the path to recovery can differ from the path to collapse as the environment changes (Scheffer et al. 2001, Scheffer and Carpenter 2003). Sources of alternative stable states within populations include Allee effects, e.g. a positive relationship between density and growth. A strong Allee effect creates an Allee threshold of population density, where collapse will occur if the population density falls below that threshold (Dennis et al. 2016). Allee effects have been well-documented for a number of species, including marine fishes (Hutchings 2013) and increase extinction risk (Dennis et al. 2016). In systems with alternative stable states, MPAs can, theoretically, decrease the likelihood of state shifts compared to traditional fisheries management. An MPA can prevent a local population from going extinct, allowing that area to act as a source of migrants to harvested areas (Barnett and Baskett 2015, 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 interaction occurs as disturbances have the potential to push populations below an Allee threshold, causing a shift to an unfavorable alternative state. This builds on work by Aalto et al. (2019), who demonstrate the buffering capacity of MPAs given disturbance and Allee effects, to explore the question of optimal spacing in a reserve network. Finally, we examine a spatially-explicit, multiple patch model of a coastline to explore the robustness of conclusions from the two-patch scenario. In addition, we use this spatially-explicit model to explore the role of fishing on network design and the effect of different management objectives, fishing versus conservation on the optimal spacing between reserves.

Methods and models

Two-patch model

First, we use a two-patch, coupled Beverton–Holt model where fished areas are included implicitly. In patch i , $N_i(t)$ is

the population size at time t . During each time step, we model three sequential events: 1) production, 2) dispersal and 3) disturbance (Fig. 1). We incorporate density-dependence in production with a Beverton–Holt function, G_i , where $r_i(t)$ is the growth factor and K_i is a population saturation parameter with a corresponding per-patch carrying capacity is $(r_i - 1)K_i$. We describe r_i as a normal distribution to allow temporal variability in the growth factor with mean μ_r and variance σ_r^2 . 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). In addition to negative density dependence arising from K_i , we incorporate the potential for Allee effects with the factor ω where an Allee effect is present (initially concave relationship between G_i and $N_i(t)$) for $\omega > 1$ (Fig. 1b). This Allee effect alters the recruitment curve, causing decreases in productivity when $N < 1$ and increases in productivity when $N > 1$ (Fig. 1b). Alternative models of

a Beverton–Holt model with Allee effects are also possible (Gaut et al. 2012). The growth function for each patch is then:

$$G_1 = \frac{r_1(t) N_1(t)^\omega}{1 + N_1(t)^\omega / K_1}$$

$$G_2 = \frac{r_2(t) N_2(t)^\omega}{1 + N_2(t)^\omega / K_2}$$

We connect the two patches via the dispersal, with fraction e of dispersing individuals (Fig. 1c). This results in a spatially-implicit model as the spatial structure between the reserves is not considered (Perry and Enright 2007). 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:

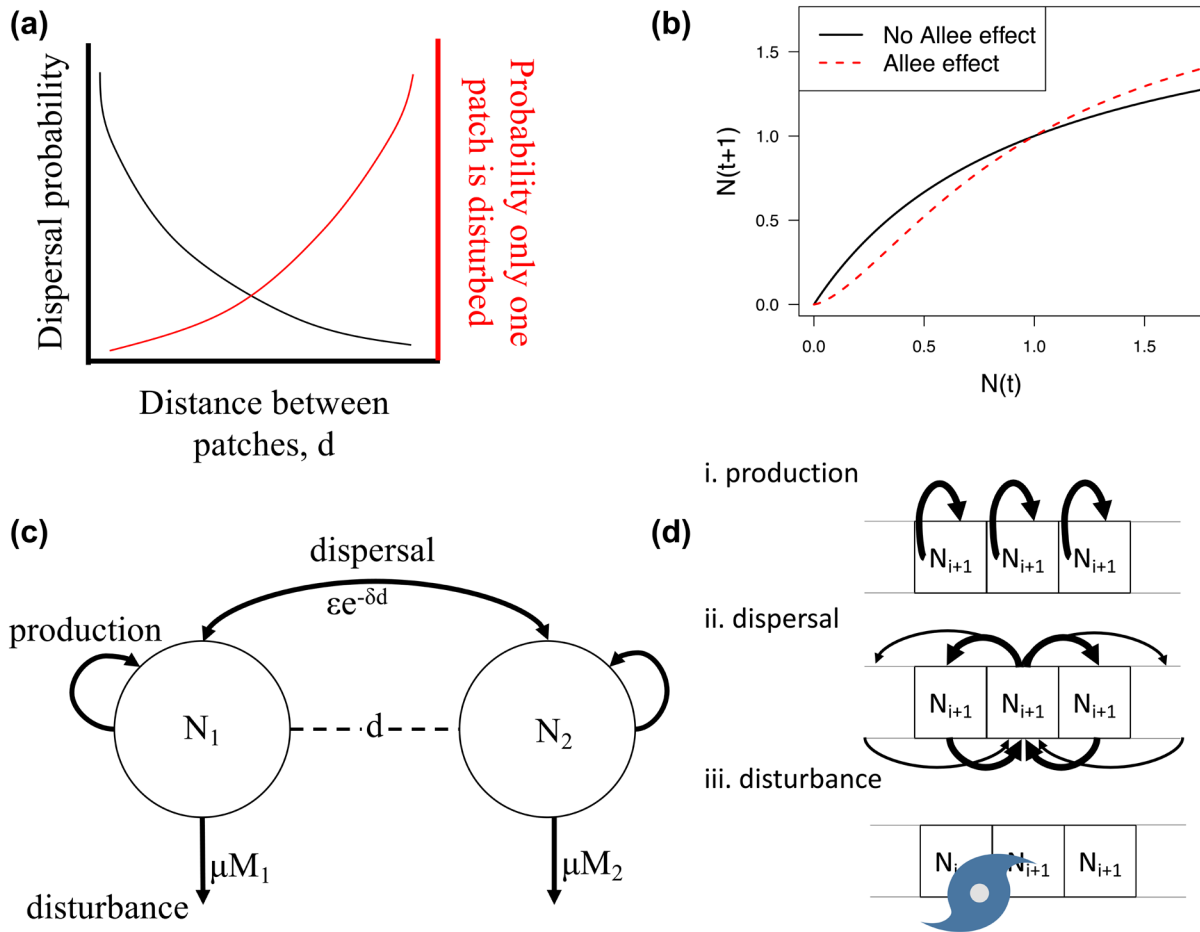


Figure 1. (a) Conceptual tradeoff between successful dispersal probability and probability that a given disturbance only affects a single patch locally for different distances between patches, d . (b) Production functions for population size from year t to year $t + 1$ without ($\omega = 1$) and with ($\omega = 1.5$) an Allee effect. (c) Model diagram for the two-patch reserve scenario. Here N_i is the abundance in patch i , μM_i 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. (d) Model for n -patches cycles through production within patches (given by the self-arrow), dispersal between patches (denoted by arrows connecting patch), and a disturbance centered on the middle patch that also affects the nearby patch to the left.

$$N'_1(t) = (1 - \epsilon)G_1 + \epsilon e^{-\delta d}G_2$$

$$N'_2(t) = (1 - \epsilon)G_2 + \epsilon e^{-\delta d}G_1$$

Finally, we model disturbance in each patch, M_p , as a binomial distribution with probability, p_i . If disturbance affects one patch, the other patch has a probability $e^{-\gamma d}$ of also being affected by the disturbance, where γ is a shape parameter. For simplicity, we only allow one disturbance event per timestep. Therefore, the disturbance occurrences are:

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

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

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 is:

$$N_1(t+1) = (1 - \mu M_1(t))N'_1(t)$$

$$N_2(t+1) = (1 - \mu M_2(t))N'_2(t)$$

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

n-patch model

We also explore a related model of n patches, which allows for spatially-explicit dynamics (Fig. 1d). We focus on a coastline system with a simple one-dimensional landscape (Fig. 1d). Thus, we examine a set of discrete, contiguous patches with some patches designated as reserves (e.g. the reserve fraction of the coastline) and other patches exposed to fishing (Botsford et al. 2001). The within-patch production function

is the same as the two-patch model, but with added fishing mortality in unprotected areas after dispersal occurs. The n -patch model allows for more biological realism with spatially-explicit representation of both dispersal and disturbance. To model dispersal, we use a geometric distribution as a discrete-space dispersal kernel with an analogous shape to the continuous exponential-decay dispersal function used in the two-patch model. To model disturbance, we randomly draw the likelihood of a given patch experiencing disturbance as a binomial variable. For the initial explorations here, and for computational simplicity, we focus our analysis on set disturbance size (the focal patch and its two neighbors, so a size of three patches). The effect of varying disturbance size (the spatially-explicit analogue to the effect of disturbance in one patch affecting the other in the two-patch model), analogous to exploring the effect of the disturbance in one patch affecting the other in the two-patch model, warrants future investigation. We describe this n -patch model fully in the Supporting information.

Reserve network optimization

Two-patch model

For the two-patch model, we examined all possible distances (at integers up to 100 units apart) between patches. With the default dispersal and disturbance parameters, distances of greater than 100 units were never optimal. The optimal spacing was the distance that maximized population persistence (proportion of runs where the ending total population size is positive). Stochasticity was low in the default model (Table 1), so only 100 runs of each parameter combination were needed.

n-patch model

In the n -patch model, we examined two different management goals for determining the optimal reserve configuration: 1) maximize the probability of population persistence, measured as the proportion of runs that end in positive population size and 2) maximize the total fisheries yield, which is the total catch over the entire time series. We then

Table 1. Parameter notation, description and default values for the two-patch model. As a sensitivity analysis, several parameters (e.g. d , ω) are varied in the Fig. 2, 3, Supporting information. The n -patch model is described more fully in the Supporting information.

Notation	Description	Default value (units)
$r_i(t)$	Growth factor of patch i at time t described as a normal distribution	
μ_r	Mean of growth factor normal distribution	3
σ_r^2	Variance of growth factor normal distribution	0.25
K_i	Population saturation parameter for patch i	1
ω	Allee effect parameter	1 for no Allee effect or > 1 for Allee effect
ϵ	Fraction of dispersing individuals	0.5
d	Distance between patches	0–100 (spatial units)
δ	Dispersal success parameter (larger δ indicates lower survival)	0.01 (1/spatial unit)
p_i	Probability of disturbance	0.02
γ	Decay parameter for probability that disturbance in one patch affects the other	0.1 (1/spatial unit)
μ	Density-independent mortality from disturbance	0.8
F	Fishing mortality rate (1 for all non-MPA patches in scorched-earth scenario)	1

examine different reserve configurations to determine the optimal spacing between reserves. For example, a system with 12 discrete patches, including three reserves, could be NNNRNNRNNRNNN where R and N represent reserve and non-reserve sites, respectively. In this example, the average spacing between reserves is $\frac{1+2}{2} = 1.5$. We examine all the possible orderings of reserves and non-reserves for a 20-patch system. Thus, we systematically examine all possible reserve networks. This is possible when the number of patches is small. This also allows us to examine specific reserve configurations instead of assuming all reserves are equally-spaced. We limit the fraction of area that can be placed in reserves, specifically 15% of the patches (we test the robustness of our results to different parameter values in Supporting information). For the baseline scenario, we examine three reserves across 20 patches for all the simulations. For each network configuration, we run 100 simulations to account for stochasticity in model runs generated by the random disturbance locations and frequencies (example dynamics in Fig. 2). We then calculate the mean value of persistence and total fisheries yield across these simulations to determine the performance of that

reserve network. We chose a set of parameters that are biologically-realistic compared to other fisheries (Britten et al. 2016) and lead to a space where certain key dynamics (e.g. tradeoff between catastrophes and connectivity) are relevant. We examine the sensitivity of our results to changes in each of the parameters (Supporting information).

Results

We find that catastrophes can increase the optimal spacing between a pair of reserves (Fig. 3a). To maximize population persistence, some spacing between patches is optimal (Fig. 3a) whenever catastrophes are present. However, as the disturbance frequency or magnitude increases, the population size (and population persistence) decreases. Thus, the optimal spacing between reserves increases with disturbance frequency, but when disturbances are too frequent the population goes extinct from the catastrophes (Fig. 3a). 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

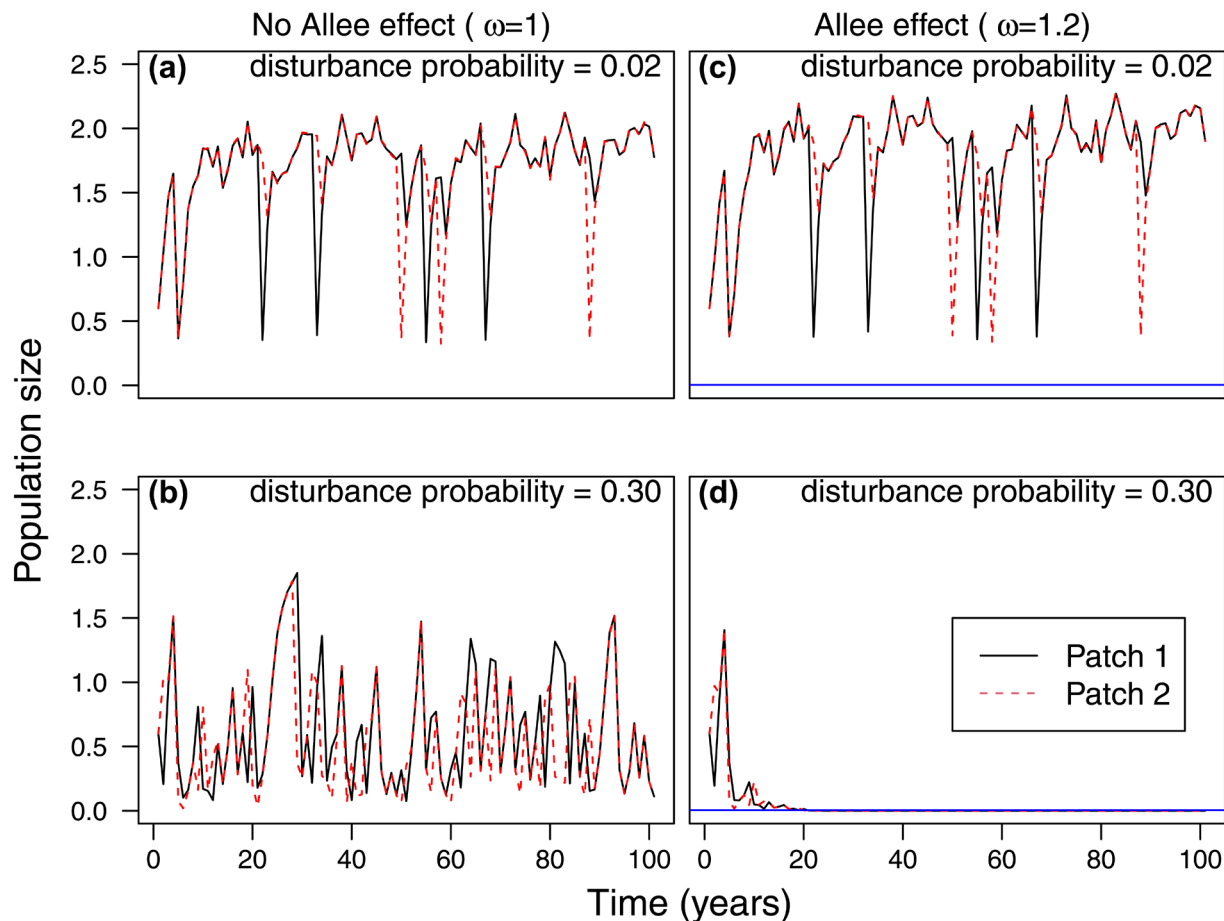


Figure 2. Example two-patch model simulation, each line denotes a different patch. The four panels represent different combinations of disturbance frequency and the presence ($\omega > 1$) or absence of an Allee effect. The horizontal line denotes the Allee threshold. The simulation is with the following model parameters: $r = 3.0$, $K = 1$, $\delta = 0.01$, $\epsilon = 0.5$, and distance between patches of 40.

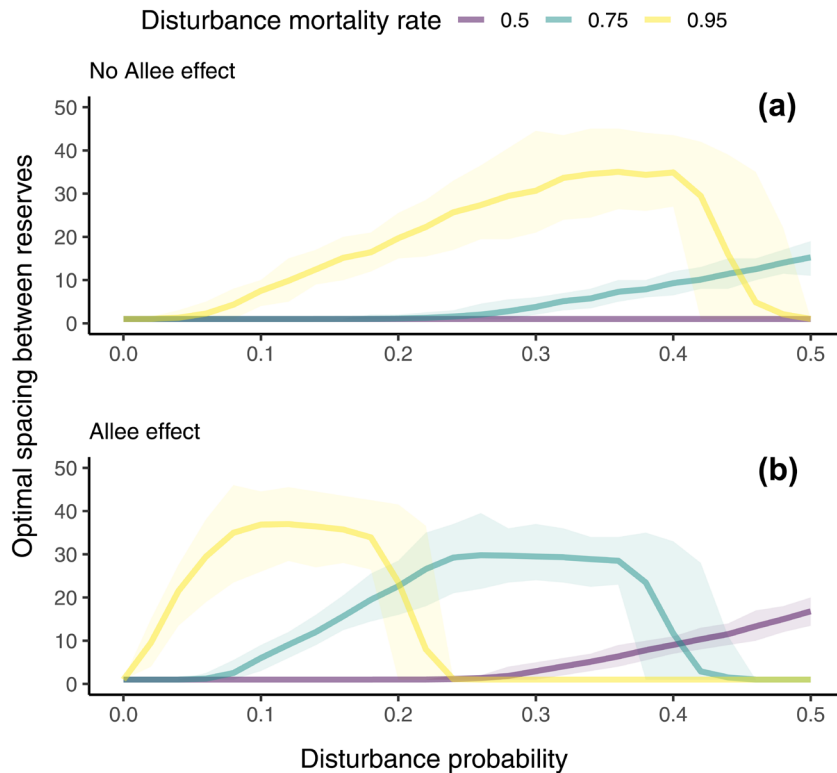


Figure 3. Average optimal spacing (solid line) and corresponding 95% confidence band (shaded area around each solid line includes 95% of model simulations) for different disturbance frequencies and mortality rates in the two-patch model. Optimal spacing to maximize persistence for the Beverton–Holt model (a) without ($\omega = 1$) and (b) with an Allee effect ($\omega = 1.2$). Each line indicates a different disturbance mortality rate. These simulations are with the same model parameters as in Fig. 2. 100 simulations were run for each parameter combination. The same figure is presented in Supporting information for with fishing yield as the objective.

strategy to maximize population persistence is to place the reserves adjacent to each other (Fig. 3a).

The presence of an Allee effect interacts with catastrophes to increase the risk of extinction (Fig. 2c–d), which decreases optimal spacing between reserves (Fig. 3b). In addition, disturbance level, once present and mortality rate have a weaker effect on optimal spacing when we account for Allee effects (Fig. 3b). In addition, the intrinsic rate of growth (r) can also modify the interaction between the Allee effect and the disturbance mortality level (Supporting information). Optimal spacing for fisheries yield (total amount of spillover from reserves given ‘scorched earth’ assumption) is similar to that for persistence, but some spacing is always optimal for fisheries yield (Supporting information).

Intuitively, the optimal distance between reserves increases with higher dispersal success, including dispersal at longer distances (Fig. 4, Supporting information). Dispersal has the strongest effect on reserve spacing at low disturbance probabilities and consequently small inter-patch distances are optimal unless there is a high probability of successful dispersal (Fig. 4). Conversely, when disturbances are likely to occur in both patches simultaneously it is optimal to space reserves closer together (Fig. 4). This happens because disturbances are large enough to drive the entire reserve network to extinction regardless of the organism’s dispersal ability. Increasing

the probability of dispersal (ϵ) decreases the optimal spacing between reserves, especially at low dispersal survival probabilities (Supporting information).

n-patch model

As with the two-patch model, optimal spacing for persistence depends on disturbance level, where the optimal spacing ranges from adjacent under no disturbance to distant under high disturbance (Fig. 3, 5, Supporting information). In addition, optimal spacing for fisheries and conservation goals diverge under no disturbance and converge with disturbance (Fig. 5, Supporting information). Without disturbances, maximizing fisheries spillover can be achieved through spreading out reserves. However, in order to maximize population persistence, it is optimal to have no reserve spacing, i.e. a single, larger reserve. For moderate disturbance frequencies, the optimal spacing between reserves can be nearly the same for the fishing and persistence objectives (Fig. 5). With increasing fraction of coastline protected, disturbances are less important and the optimal distance between reserves peaks at higher disturbance probabilities (Supporting information). As with the two-patch model, including an Allee effect increases optimal spacing for persistence compared to the case with no Allee effect (Supporting information).

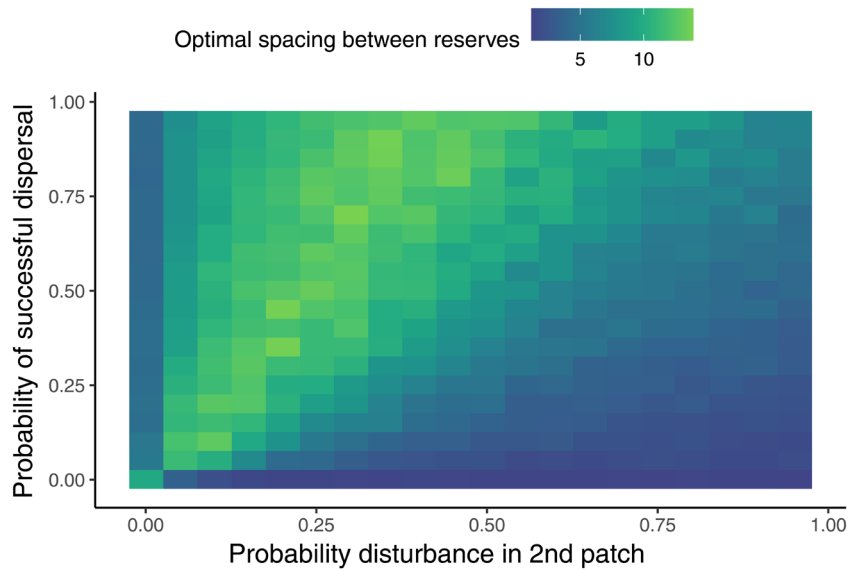


Figure 4. The optimal spacing between reserves for population persistence given different combinations of successful dispersal probability and the probability that a disturbance in one patch affects the nearby second patch (i.e. γ and δ are varied to produce the linear probabilities shown on axes for an inter-patch distance of 50). Simulations here are for a two-patch model with an Allee effect ($\omega = 1.2$) and the same parameter values as in Fig. 2.

However, the optimal spacing for fisheries yield is greater without Allee effects (due to greater spillover with greater persistence likelihood) and the optimal spacing for fisheries and persistence converge more slowly as disturbance increases (Supporting information).

All of the two-patch 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 (Fig. 6). At high disturbance frequencies, this relationship reverses and reduced fishing

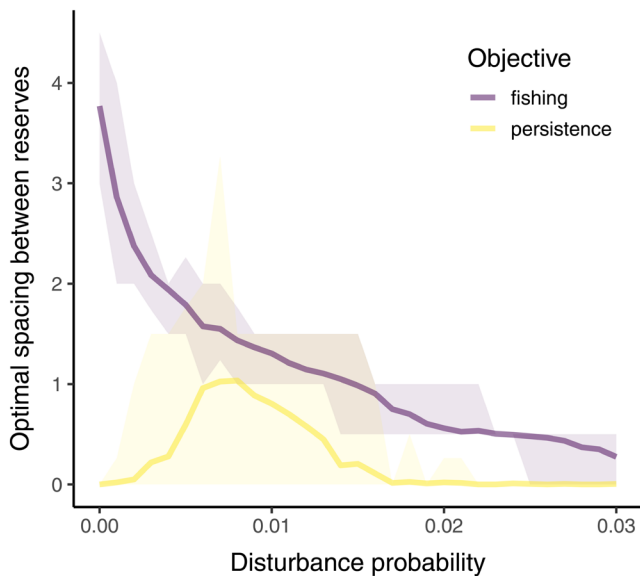


Figure 5. Average optimal spacing (solid line) and corresponding 95% confidence band (shaded area around each solid line includes 95% of model simulations) in an n-patch model versus the probability of disturbance (which is smaller than the two-patch model to keep per-patch disturbance rates constant) for two different objective functions. The parameter values used are: $\delta = 0.7$, $\omega = 1.2$, $r = 3$ and $\mu = 0.95$. The same figure is presented in the Supporting information except for $\omega = 1.0$.

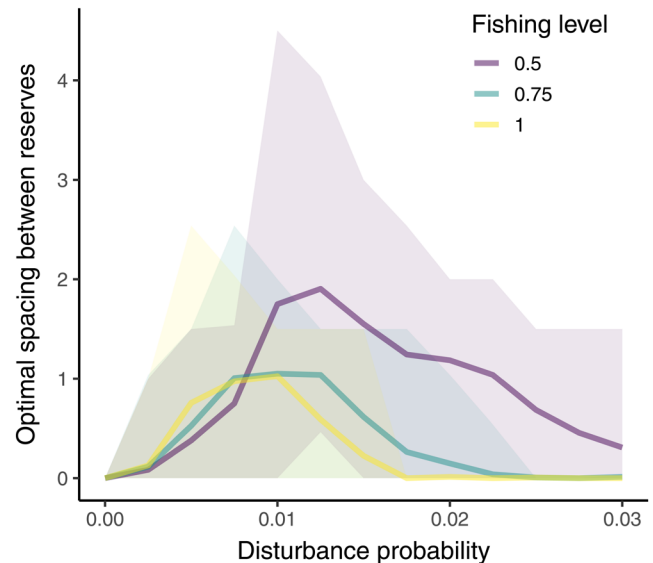


Figure 6. Average optimal spacing (solid line) and corresponding 95% confidence band (shaded area around each solid line includes 95% of model simulations) in an n-patch model to maximize persistence for different disturbance frequencies and fishing levels outside of reserves (fraction of population harvested in each patch). The parameter values used here are: $\delta = 0.7$, $\omega = 1.2$, $r = 3$ and $\mu = 0.9$.

pressure increase the optimal spacing between reserves (Fig. 6). This happens because fishing pressure outside reserves reduces the capacity for the system to recover from catastrophes.

To further examine the specific reserve network configurations, we focus on an intermediate disturbance probability (0.01) because of the greater variation in optimal reserve configuration at that value (Fig. 5). Examining 20 different optimal reserve configurations, we found that the density of reserve locations were clustered together. However, this does not mean that zero spacing was the most optimal. Instead, the most common spacing in this example was zero spacing between two reserves and a spacing of three for the third reserve (Fig. 7).

Discussion

Disturbances can increase the spacing in reserve networks to achieve an objective of maximizing persistence (Fig. 3, 5). The optimal distance is a tradeoff between the disturbance size and frequency as well as the dispersal ability of the organism. These results are in line with that of Wagner et al. (2007), who found that persistence was maximized at intermediate inter-reserve distances because of the same set of tradeoffs. We expand their findings with our consideration of density dependence and fisheries outside reserves, where we find that

persistence is not always maximized with spacing between reserves. Instead, the exact spacing depends on the specific disturbance regime and the life history (i.e. dispersal) of the species. Our results are most analogous to situations where disturbances directly cause additional mortality, for instance hurricanes and oil spills (Allison et al. 2003). If disturbances are not frequent, or only have a marginal effect on survival rates, it will still be optimal to place reserves nearby one another to maximize connectivity (Fig. 3, 5).

The benefit to spacing out reserves, for potential post-disturbance rescue across a reserve network, is most relevant to long-distance dispersers, and short-distance dispersers do not experience this benefit in our model (Fig. 4). In the extreme, our results with short-distance dispersal approach the model without dispersal by Game et al. (2008b), who found that protecting larger reserves was more optimal than smaller, spread out reserves when catastrophes are present. McGilliard et al. (2011) explicitly modeled dispersal, making their models most akin to our own. In the presence of disturbances, they found that persistence was unlikely if only a marine reserve was the only spatial management strategy. We build on this work by showing that persistence is possible using a network of reserves, as opposed to a single large reserve. Thus, we see that if the probability of successful dispersal is higher than the probability of disturbance affecting reserves simultaneously, then it is always optimal to spread out reserves when disturbances are present (Fig. 4).

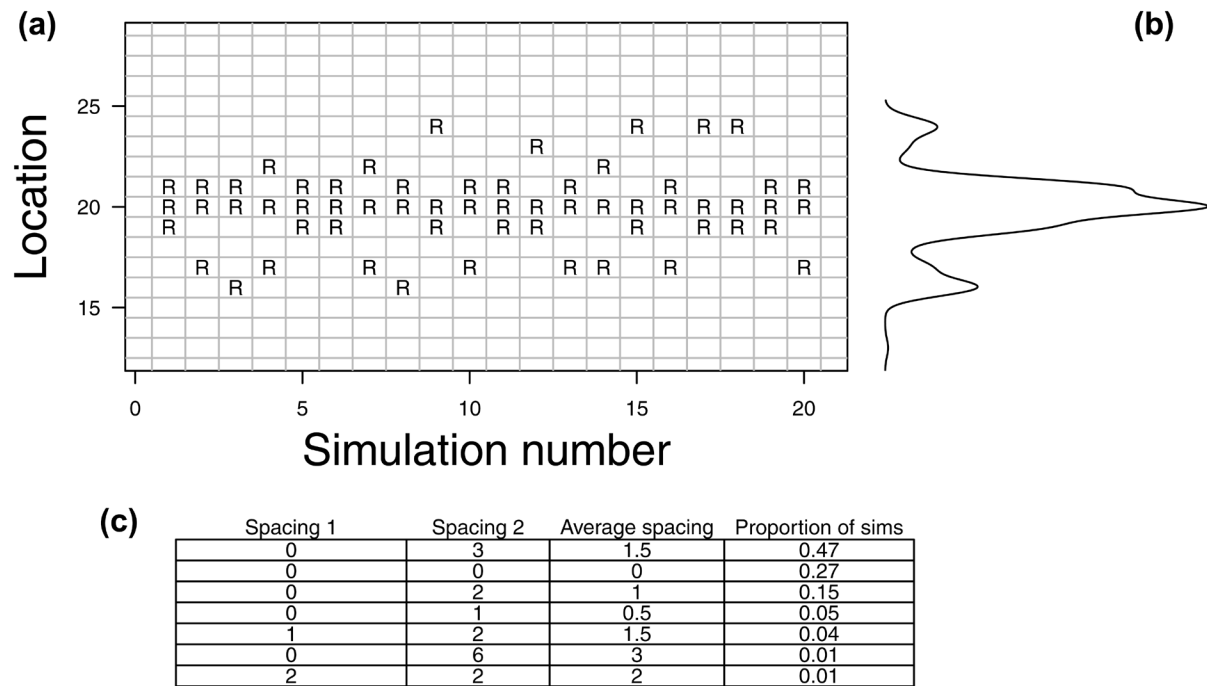


Figure 7. (a) Reserve locations for 20 different randomly-chosen simulations all using the same parameter values. These are the same parameters as Fig. 5 with a set probability of disturbance of 0.01 (a value on Fig. 5 with high variability in optimal spacing) and for the persistence objective. Each R denotes the optimal placement of a reserve for each simulation. (b) Density plot of reserve locations chosen across 100 simulations. (c) Proportion of all simulations for each reserve configuration across 100 simulations. Spacing 1 and spacing 2 columns denote individual inter-patch spacing where the average spacing is the average of spacing 1 and spacing 2. Note that the middle reserve is always centered at 20, which reduces computational time.

Including Allee effects in our model decreased persistence and increased the optimal spacing between reserves (Fig. 2d, 3b). A strong Allee effect creates alternative stable states with a tipping 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 (Fig. 3b). This increases the likelihood that acting as an insurance policy for one another plays a role in persistence. Our findings are in line with past theoretical findings on catastrophes and the distance between patches within a metapopulation (Blowes and Connolly 2012, Dennis et al. 2016) showing the robustness of our results. Thus, designing reserve networks with catastrophes in mind will be particularly relevant for species that experience mate limitations at low density or that rely on larger populations for survival (Courchamp et al. 1999). Specific examples include 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.

We found that catastrophes can lead to alignment in the optimal design of reserves networks for objectives that would otherwise trade off with each other. In analyzing different reserve objectives, we found that, at intermediate disturbance levels, the optimal spacing between reserves was similar for both maximizing fishing and maximizing persistence, especially when considering the overlap in confidence bands (Fig. 5). In comparison, we find that without catastrophes (disturbance frequency is zero), large, single reserves maximize persistence and smaller, spread out reserves maximize fishing as with other papers without disturbance (Gaines et al. 2010). This conflict arises because spreading out reserves maximizes spillover from reserves to fished areas, but reduces within-reserve protection. However, when accounting for catastrophes and Allee effects in our models, disturbances lead to an optimal reserve design where reserves are spread out in order to decrease the probability of synchronous collapse of all reserve areas and therefore increase the probability of persistent spillover.

In the two-patch simulations, fisheries yield and persistence criteria are similar because all fisheries yield comes from reserve spillover given the scorched earth assumption, but the n-patch simulation allows relaxation of that assumption for a more nuanced exploration. We found that decreasing fishing pressure outside reserves can increase the optimal spacing between reserves, even with the high variability in spacing shown by the confidence bands (Fig. 6). This happens because of higher abundance outside reserves, reducing their buffering effect. In line with our results, McGilliard et al. (2011) found that fishing management outside a single reserve was important to maximize persistence as higher abundances

with lower fishing pressure overall decreased susceptibility to local disturbances. A similar effect occurs here in terms of reduced need to space reserves apart to avoid simultaneous disturbance.

In addition to finding the optimal spacing between reserves, we also examined the optimal configuration of reserves. While many MPA models assume equally-spaced reserves for simplicity, this is not always optimal. For instance, work by Kaplan and Botsford (2005) showed that variable spacing between reserves was beneficial in situations of high fishing pressures and small reserve sizes. Our work also focused on high fishing pressure and small reserves, but with the inclusion of disturbances. We found that at intermediate disturbance rates, variable spacing can be optimal (Fig. 7). In our model, variation in reserve spacing can balance the tradeoff between decreased likelihood of simultaneous disturbance and decreased connectivity as spacing increases. In our simulations, given our focus on the particular case of disturbances of a size of three patches, the combination of 0 (adjacent reserves) and 3 (spaced exactly far enough apart to avoid simultaneous disturbances) is the most frequent optimal reserve design. Larger or variable disturbance sizes would likely increase both the magnitude and variability of optimal spacing.

In addition, these variable spacing results point to the idea that, in an uncertain environment driven by disturbances, many reserve configurations might meet the same objective. This highlights an important point of commonly-used spatial optimization approaches, including both static (e.g. MARXAN) and dynamic connectivity models (Brown et al. 2015). For example, Chollett et al. (2017) used dynamic spatially-explicit models to examine optimal placement of reserves for the Caribbean spiny lobster. They chose reserve locations that were the most frequently chosen across a large number of simulations to account for demographic stochasticity, but not disturbances. Our results show that a specific site might be chosen for a reserve often by simulations, but its optimality as a reserve location still depends on the other reserve locations chosen (Fig. 7). Further work is needed to assess the full implications of this result.

As with any model, we make a number of simplifications. First, we use a particular function for production, a Beverton–Holt with an Allee effect. Our modeled Allee effect produces higher production when $N > 1$ compared to the non-Allee effect version (Fig. 1). Other forms of the Allee effect without this property might have populations that are more susceptible to extinction given lower production in nearby patches. In addition, the patch connectivity would have to be determined using an approach like a regional oceanic modeling system (ROMS) model or other connectivity data (Shchepetkin and McWilliams 2005, Watson et al. 2012). A more realistic connectivity model might alter the optimal spacing between reserves given specific sink–source dynamics (Crowder et al. 2000) and variability in connectivity between years (Williams and Hastings 2013). More specifically, the relationship between the spatial scale of dispersal and disturbance interact to determine optimal reserve configurations

(Quinn and Hastings 1987, Kallimanis et al. 2005); this might be especially true in systems with landscapes more complex than a simple linear coastline (Moloney and Levin 1996). Further, our model includes local dispersal and local catastrophes. Actual connectivity data could decouple these processes if dispersal is on much larger scales than catastrophes. We ignore age structure, which can have a buffering effect to disturbances if age classes are affected differentially. In a system with sedentary adults, including age structure might increase the production within reserves. This, in turn, concentrates the population, increasing the importance of spacing reserves in the presence of catastrophes. Furthermore, disturbance likelihood can be spatially and temporally heterogeneous, where some parts of the coastline might experience lower-frequency disturbance (Game et al. 2008b, Mellin et al. 2016). Game et al. (2008b) found that for realistic rates of cyclones affecting the Great Barrier Reef, persistence was maximized by protecting subsets of the reef, the specific subsets depending on the cyclone frequency and the post-disturbance recovery rate. Thus, for our results on optimal spacing, heterogeneous disturbances could cause variable spacing between reserves or prioritizing of certain regions. Although there exists high quality data on the location and frequency of different disturbances (e.g. US National Hurricane Center <www.nhc.noaa.gov/data/>; Coral Reef Watch <<https://coralreefwatch.noaa.gov/>>), connecting these data to population dynamics also requires knowledge about the demographic effects (e.g. mortality rates of corals for different cyclone severity) these have on marine organisms. Further, we only focused on disturbances that act independent of the population dynamics (e.g. hurricanes). Disturbances, such as diseases, that can negatively affect population dynamics through connectivity (e.g. disease spread from dispersal) then increase the spacing expected to optimize population persistence (Sokolow et al. 2009, Kough et al. 2015). In addition, a binary function for disturbance mortality is not always appropriate. Instead, disturbance mortality as a function of distance from central area affected by the disturbance might be more accurate (e.g. hurricanes). Lastly, our study focused on a single species. For multi-species systems, species can have different life histories, including their dispersal abilities and susceptibility to disturbances. This could lead to different reserve networks for multi-species systems (D'Aloia et al. 2017), including scenarios where variable spacing or sizes of reserves might be optimal. Thus, future work should examine system-specific life-history traits and disturbance regimes as well as multiple species.

Data availability statement

Data available from the Dryad Digital Repository: <<http://doi.org/10.25338/B88635>> (White et al. 2020b).

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Author contributions

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