Spatial structure induced by marine reserves shapes population responses to catastrophes in mathematical models

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Abstract. Catastrophic events such as oil spills, hypoxia, disease, and major predation events occur in marine ecosystems and affect fish populations. Previous evaluations of the performance of spatial management alternatives have not considered catastrophic events. We investigate the effects of local and global catastrophic events on populations managed with and without no-take marine reserves and with fishing mortality rates that are optimized accounting for reserves. A spatial population dynamics model is used to explore effects of large, catastrophic natural mortality events. The effects of the spatial spread, magnitude, probability of catastrophe, and persistence of a catastrophic event through time are explored. Catastrophic events affecting large spatial areas and those that persist through time have the greatest effects on population dynamics because they affect natural mortality nonlinearly, whereas the probability and magnitude of catastrophic events result in only linear increases in natural mortality. The probability of falling below 10% or 20% of unfished abundance was greatest when a no-take marine reserve was implemented with no additional fishing regulations and least when a no-take marine reserve was implemented in addition to the maintenance of optimal fishing mortality in fished areas. In the absence of implementation error, maintaining abundance across space using restrictions on fishing mortality rates, regardless of the existence of a no-take marine reserve, decreased the probability of falling below 10% or 20% of unfished abundance.

Key words: catastrophes; catastrophic events; extinction threshold; fisheries management; marine protected areas; no-take marine reserve; population dynamics; spatial modeling; total allowable catch.

INTRODUCTION

Although not often explicitly included in models of population dynamics, catastrophes (reductions in population size of 60% or greater) can drive the population viability of flora and fauna (Menges 1990, Mangel and Tier 1994). Oil spills, harmful algal blooms, hypoxia, sudden changes in trophic dynamics, and the appearance of invasive species are examples of potential causes of catastrophes. Ward et al. (2007) estimated that catastrophes cause 75% decreases in fur seal pup abundance. Similarly, Gerber and Hilborn (2001) detected catastrophes causing population declines of greater than 50% in numerous data sets for fur seals and sea lions. In addition, long-term evidence from widely publicized events, such as the Exxon Valdez oil spill (Peterson et al. 2003) and the introduction and subsequent spread of the zebra mussel to the Great Lakes (Strayer and Malcom 2007), suggests the importance of considering ways to account for the effects of catastrophes when investigating tools for managing marine life.

No-take marine reserves (NTMRs) are thought to alter population responses to catastrophes and other uncertainties (e.g., Lauck et al. 1998, Mangel 2000, Allison et al. 2003, Halpern et al. 2006). Two common conclusions from previous investigations of population responses to NTMRs in the presence of uncertainty are that NTMRs lower the probability of falling below extinction thresholds (Mangel 2000, Rodwell and Roberts 2004) and decrease variability in catches (Lauck et al. 1998, Mangel 2000, Rodwell and Roberts 2004). The conclusions of these studies hinge critically on the assumptions made about population and fishery dynamics. The similarity in model structures and assumptions among these papers potentially limits the ability to generalize their results. Here we identify six common model assumptions from previous analyses about the role that NTMRs play in mediating population responses to catastrophes, and then develop a more general framework for exploring this question.

1) All models consider two or three areas in which one or more areas represent an NTMR. This masks spatial structure in the population, affecting the efficiency of the fishery and survival when mortality is density dependent.
2) Mortality does not depend on local density in many studies (e.g., Mangel 2000, Halpern et al. 2006, Wagner et al. 2007). This means that the abundance in a single area can grow unchecked by the limitations of the local habitat in the event of a productive
regime, especially in areas without fishing. This potentially enhances the success of NTMRs beyond realistic biological limits.

3) Some studies include fluctuations in catch, which can also be seen as “implementation errors” associated with an inability to enforce regulations related to specified fishing mortality or total allowable catch (TAC) levels. Fluctuations in catch have the potential to be a key source of uncertainty. However, the influence of implementation error has not been distinguished from that of other sources of uncertainty in previous studies (Mangel 2000, Rodwell and Roberts 2004). Fluctuations in catch affect fishable areas only and will augment the buffering effect of NTMRs because the additional mortality that is inflicted is directly avoided by implementing NTMRs. Therefore, NTMR implementation will cause catch to decline, but will also reduce fluctuations in catch.

4) Most uncertainties that are modeled impact individuals throughout the spatial range of a population, and therefore do not consider uncertainties that occur on smaller spatial scales, affecting only individuals in selected areas of a population’s range. For example, an oil spill or shortage of prey could impact parts of a species range while leaving other areas unaffected. We hypothesize that NTMRs will provide a buffer against catastrophes when catastrophes affect all parts of a species’ range equally because a greater number of individuals will survive a catastrophe that kills a constant proportion of individuals in each area, leaving some abundance to ensure population viability.

5) Models that include intermittent catastrophic adult mortality do so only by considering populations in a fished state and do not consider the effects on populations in an unfished state (Rodwell and Roberts 2004, Holland and Stokes 2006). This means that the long-term size of a population would not equal the value expected given deterministic considerations and the absence of fishing if catastrophes were to occur when the population was unfished. This is important because most fisheries reference points are based on comparisons of fished vs. unfished population levels. Thus, the failure to properly adjust unfished population size to the same catastrophe characteristics exaggerates the impacts of catastrophes on a fished population (Rodwell and Roberts 2004, Holland and Stokes 2006).

6) In many studies, a fishery with high fishing mortality prior to the establishment of an NTMR is simulated and population viability with NTMRs is compared to when no management action is taken (Lauck et al. 1998, Mangel 2000, Halpern et al. 2006, Wagner et al. 2007). Deterministic models of NTMRs have established that implementing an NTMR will increase population abundance and cause the population to remain extant if a fishery is overfished (e.g., Holland and Brazee 1996, Gerber et al. 2003, Hilborn et al. 2006). Stochastic models are similar in structure to deterministic models, except that there are terms representing stochasticity. These models show the same results as deterministic models with similar model structure, which suggests that model structure, not stochasticity, determines the outcomes of the analyses. Previous studies were not designed to disentangle the role of stochasticity from that of model structure.

Many of the studies just discussed explore the efficacy of NTMRs in unregulated fisheries. However, NTMRs are sometimes established in regulated fisheries that are not overfished. A growing body of work (Rodwell and Roberts 2004, Hilborn et al. 2006, Holland and Stokes 2006, McGilliard and Hilborn 2008) shows that the state of the fishery, regulations outside reserve borders, and spatial connectivity among populations are key variables in determining the effects of an NTMR on population abundance, catch (yield), and CPUE (catch per unit effort). Each of these variables interacts with NTMRs to affect the spatial structure of the population, which in turn affects local population dynamics and fishing behavior.

The spatial patterns that would lead to catastrophes increasing vs. reducing population viability and other common performance measures (such as catch variability) have not yet been explored fully. We therefore develop extensions of previous models to address this issue as well as the issues previously raised.

The goal of this paper is therefore to evaluate the effects of NTMRs as fishery management tools in the presence of catastrophes. We consider two scenarios: (1) populations that are managed optimally with and without an NTMR and (2) populations that are declining, and one of two management alternatives are implemented, both of which produce the same population abundance over time under deterministic conditions. These two alternatives are an NTMR or a TAC. In all cases, we compare the outcomes of alternative management strategies in the presence of catastrophes that differ with respect to spatial (local or global) and temporal extent (punctuated or persistent). We also explore the impact of uncertainty when determining TACs, i.e., implementation error.

**Methods**

**Modeling biology, fishing regulations, and the dynamics of the fishing fleet**

Population dynamics, fishery dynamics, and fishery regulations are specified in Appendix A. We used a spatial population dynamics model (a metapopulation model) with 100 consecutive areas. Population dynamics were modeled within each area and were divided into two life history stages: larvae and adults. Areas were connected via larval dispersal whereby adults were sedentary and larvae dispersed as a decreasing function.
of distance from a natal area. After dispersal, larvae recruited to the adult population according to a Beverton-Holt stock–recruitment relationship (e.g., post-dispersal density-dependent mortality; Hilborn and Walters 1992, McGilliard and Hilborn 2008). Larval dispersal distance was medium (\( m = 13 \) areas; Fig. 1) in our simulations. This is because maintenance of catch is a typical objective determining management regulations for fisheries, and McGilliard and Hilborn (2008) show that catch is small if larval dispersal is short for a population in decline regulated solely using an NTMR.

Boats concentrated in areas of highest adult abundance in each time step and fishing was regulated by a TAC in which fishing fleets caught up to a specified fraction of the population. No fishing occurred inside NTMRs.

**Modeling catastrophes**

Typically, all natural mortality is represented in fisheries population dynamics models as a constant instantaneous rate, independent of area. In this paper, we defined catastrophes as intermittent mortality events that exist in addition to a constant instantaneous non-catastrophic rate of natural mortality (\( \beta \)); the additional catastrophic mortality rate was \( \alpha_{i,t} \) and the total instantaneous mortality rate in area \( i \) at time \( t \) (\( M_{i,t} \)) was

\[
M_{i,t} = \beta + \alpha_{i,t}.
\]

(1)

Five factors determined the occurrence and characteristics of a catastrophe: the epicenter of the catastrophe, which was one of the 100 areas (\( \gamma \)); the size of the affected area (modeled in Eq. 2 as a function of the standard deviation of a discrete normal distribution over space, \( \sigma_{\text{cat}} \)); the probability of catastrophe (\( \phi \)); the magnitude of the catastrophe at its epicenter (\( \xi \)); and the amount of time that natural mortality was amplified by the catastrophe (characterized by \( \rho \), the correlation in the catastrophic mortality from one time step to the next in the absence of a new catastrophe). Thus, the additional mortality caused by a catastrophe was

\[
\alpha_{i,t} = \begin{cases} 
\alpha_{i,t-1} + \xi \exp \left[ \frac{(i - \gamma)^2}{2\sigma_{\text{cat}}^2} \right] & \text{if } \kappa_i < \phi \\
\alpha_{i,t-1} + \xi & \text{otherwise}
\end{cases}
\]

(2)

where \( \kappa_i \) is a random number chosen from a uniform distribution \( U [0, 1] \). We adjusted non-catastrophic mortality so that the average unfished abundance with and without catastrophes was the same. Thus, a different value for \( \beta \) applied to each set of parameters characterizing catastrophes. We found this value so that the unfished equilibrium in the absence of catastrophes and the average adult abundance over 100 simulations with catastrophes were the same.

![Fig. 1. Dispersal kernel of larval fish from area 50 to surrounding areas for a single time step.](image)

**Analytical development: properties of the catastrophic mortality equation**

The expected catastrophic mortality rate over time is

\[
\alpha_t = \alpha_0 + \phi \xi \exp \left[ \frac{(i - \gamma)^2}{2\sigma_{\text{cat}}^2} \right].
\]

(3)

Rearranging and substituting \( d = i - \gamma \) where \( d \) is the distance from the epicenter of a catastrophe gives

\[
\alpha_d = \frac{\phi \xi \exp \left[ \frac{-d^2}{2\sigma_{\text{cat}}^2} \right]}{1 - \rho}.
\]

(4)

Each parameter in Eq. 4 affects the catastrophic mortality rate in a different way. Increases in time-averaged catastrophic mortality, \( \alpha_d \), are a linear function of the probability (\( \phi \)) or magnitude (\( \xi \)) of catastrophe. However, increases in \( \alpha_d \) are nonlinear functions of the temporal autocorrelation (\( \rho \)) and spatial spread of catastrophe (\( \sigma_{\text{cat}} \)).

The expected value of the catastrophic mortality, averaged over time and space, is

\[
\alpha = \frac{1}{100} \sum_{d=0}^{100} \frac{\phi \xi \exp \left[ \frac{-d^2}{2\sigma_{\text{cat}}^2} \right]}{1 - \rho}.
\]

(5)

**Simulating catastrophes**

Eq. 5 was solved for the probability (\( \phi \)) and magnitude (\( \xi \)) of a catastrophe such that the average catastrophic mortality (\( \alpha \)) remained the same for each simulation and was equal to half of the total average mortality, \( M \) (\( \alpha = 0.05 \); \( M = 0.10 \)). Parameter values for non-catastrophic natural mortality (\( \beta \)) are listed in Appendix B: Tables B.1 and B.2. The probability and
magnitude of a catastrophe have the same mathematical effect, so we assumed that their values were equal (i.e., $\phi = \xi$). We simulated global catastrophes by specifying that the spatial spread of the effects of a catastrophe about its epicenter was extensive ($\sigma_{\text{cat}} = 50$ areas). Global catastrophes were simulated with and without temporal autocorrelation ($\rho = 0.5, \phi = \xi = 0.204$; and $\rho = 0, \phi = \xi = 0.288$, respectively). In addition, we simulated local catastrophes by specifying that the effects of a catastrophe about its epicenter extended to only a few areas ($\sigma_{\text{cat}} = 10$ areas); local catastrophes were simulated with and without temporal autocorrelation ($\rho = 0.5, \phi = \xi = 0.483$; and $\rho = 0, \phi = \xi = 0.620$, respectively) for a total of four unique types of catastrophe. For each catastrophe type and each management strategy, we simulated a scenario in which the TAC was implemented perfectly ($\sigma_{\text{opt}} = 0$) and in which there was log-normal implementation error ($\sigma_{\text{opt}} = 0.5$):

$$\text{TAC}_t = \left( \bar{s}_t \sum_i N_{i,t} \right) \exp(\omega_t - \sigma_{\text{opt}}^2/2)$$

$$\omega_t \sim N(0, \sigma_{\text{opt}}^2)$$  \hspace{1cm} (6)

where $s_t$ was the exploitation rate used to determine the TAC$_t$ and $N_{i,t}$ was the adult abundance in area $i$ at the start of time step $t$.

**Management scenarios**

The simulations were run for 30 time steps before the management strategies were implemented for a further 100 time steps; 1000 simulations were performed for each scenario. We simulated four management strategies, shown in Table 1: (1) a population managed at the TAC that produces maximum sustainable yield (MSY), without an NTMR ($s_{r>30} = s_{\text{MSY}}$; Table 1); (2) a population managed with a single NTMR of 20% of the coastline and regulated by an optimal value for the exploitation rate, $s_{r>30} = s_{\text{opt}}$, accounting for the NTMR ($s_{\text{opt}}$ was found by running stochastic simulations with the specified NTMR and finding the value of $s_{r>30}$ that maximized the catch in time step 100 over all simulations; see Table 1); (3) a population that is in decline (managed with a TAC based on $s_{r>30} = s_{\text{high}}$) prior to the implementation of an NTMR of 20% of the coastline with no reduction in the TAC ($s_{r>30} = s_{\text{high}}$; see Table 1); and (4) a population that is in decline prior to the implementation of a lower TAC ($s_{r>30} = s_{\text{equiv}}$; Table 1). The parameter $s_{r>30}$ for management strategy 4 was set so that TAC-based management led to the same adult abundance after 100 time steps as implementing an NTMR under deterministic conditions ($s_{r>30} = s_{\text{equiv}}$; that is, non-catastrophic mortality accounted for 100% of the natural mortality and there was no implementation error). Thus, differences in, for example, the distributions of adult abundance among management strategies were a result of how the population responded to catastrophes under each management strategy (NMTR vs. TACs), rather than the performance of each management strategy under deterministic conditions. For simulations of a fishery that is in decline, we applied a high initial fishing mortality rate ($s_{0.10} = 0.19$; note that $s_{\text{MSY}}$ is produced by $s = 0.10$ with no NTMR) for 30 time steps. The random numbers, $\kappa_t$, governing catastrophes were the same for each management strategy to maximize comparability among the results.

**Performance measures**

We assessed the short- and long-term performance of each management strategy for each scenario by evaluating the probability that the total adult abundance (over space) fell below 10% or 20% of unfished abundance (arbitrary levels that define population sizes below which management would not like to go) over 20
and 100 time steps. We also compared average abundance, catch, and CPUE for each scenario after 100 time steps, as well as interannual and inter-simulation variation (coefficient of variation, CV) in catch and CPUE.

**RESULTS**

*Declining fishery with no implementation error*

Implementing a lower TAC consistently resulted in lower probabilities of falling below 10% of unfished abundance than implementing an NTMR, irrespective of whether catastrophes were local or global (Table 2, Fig. 2b, d), even though the two strategies produced equal adult abundances in the absence of catastrophes and other uncertainties after 100 time steps (Table 2).

*Optimal fishery with no implementation error*

Regardless of the properties of the catastrophe, general trends in adult abundance, catch, and CPUE emerged from simulations with optimal management strategies with and without NTMRs. Adult abundance and CPUE were consistently higher and catch was consistently lower with an NTMR (Table 3). The occurrence of higher CPUE when there is an NTMR and management is optimal (Table 3) is different from the results of previous studies in which fisheries were managed at $F_{MSY}$ prior to the implementation of an NTMR and no adjustments were made in the TAC when an NTMR was implemented (nonoptimal management; Hilborn et al. 2006, McGilliard and Hilborn 2008).

The probability of falling below 10% of unfished abundance is very low for a fishery that is managed at $F_{MSY}$ prior to the start of simulations and continues to be managed at an optimal exploitation rate with or without an NTMR (Fig. 2a, c). Therefore, we report the probability of falling below 20% of unfished abundance, which was lower for a fishery managed optimally with an NTMR than for a fishery managed with an optimal TAC only (Table 3). The probability of falling below 20% of unfished abundance was greater when catastrophes were global or correlated over time (Table 3).

**Spatial distribution of abundance among management strategies**

The average spatial distribution of populations varied among management strategies (Fig. 3). Managing optimally led to some animals in all areas in addition to higher densities within NTMRs after time step 100 (Fig. 3a, c), whereas managing with an NTMR led to

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### TABLE 2. Performance measures for a population that is initially overfished and in decline, under local and global catastrophes, with two levels of temporal autocorrelation.

<table>
<thead>
<tr>
<th>Management strategy and implementation</th>
<th>Temp. autocorr.</th>
<th>Prob. N &lt; 0.10N&lt;sub&gt;0&lt;/sub&gt;</th>
<th>Interannual CV of catch mean (90% intervals)</th>
<th>Average abundance (no. fish)</th>
<th>Average yield (no. fish)</th>
<th>Average CPUE</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>a) Perfect implementation of TAC ($\sigma_0 = 0$)</strong></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Deterministic model</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TAC only</td>
<td></td>
<td>0.621</td>
<td>0.34 (0.25–0.43)</td>
<td>22,682</td>
<td>29,45</td>
<td>5.94</td>
</tr>
<tr>
<td>NTMR only</td>
<td></td>
<td>0.81</td>
<td>0.40 (0.29–0.52)</td>
<td>20,945</td>
<td>23,81</td>
<td>2.38</td>
</tr>
<tr>
<td>Global catastrophes ($\sigma_{cat} = 50$ areas)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TAC only</td>
<td></td>
<td>0.58</td>
<td>0.37 (0.26–0.50)</td>
<td>22,221</td>
<td>28,63</td>
<td>5.78</td>
</tr>
<tr>
<td>NTMR only</td>
<td></td>
<td>0.798</td>
<td>0.43 (0.30–0.59)</td>
<td>20,270</td>
<td>23,06</td>
<td>2.31</td>
</tr>
<tr>
<td>Local catastrophes ($\sigma_{cat} = 10$ areas)</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>TAC only</td>
<td></td>
<td>0.243</td>
<td>0.29 (0.23–0.35)</td>
<td>22,648</td>
<td>29,11</td>
<td>6.08</td>
</tr>
<tr>
<td>NTMR only</td>
<td></td>
<td>0.740</td>
<td>0.38 (0.30–0.48)</td>
<td>19,703</td>
<td>22,50</td>
<td>2.25</td>
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<tr>
<td>TAC only</td>
<td></td>
<td>0.353</td>
<td>0.32 (0.24–0.41)</td>
<td>22,540</td>
<td>29,00</td>
<td>6.11</td>
</tr>
<tr>
<td>NTMR only</td>
<td></td>
<td>0.813</td>
<td>0.42 (0.30–0.57)</td>
<td>19,103</td>
<td>21,97</td>
<td>2.20</td>
</tr>
<tr>
<td><strong>b) Error in implementation of TAC ($\sigma_0 = 0.5$)</strong></td>
<td></td>
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</tr>
<tr>
<td>Global catastrophes ($\sigma_{cat} = 50$ areas)</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>TAC only</td>
<td></td>
<td>0.770</td>
<td>0.56 (0.49–0.65)</td>
<td>20,043</td>
<td>27,85</td>
<td>5.20</td>
</tr>
<tr>
<td>NTMR only</td>
<td></td>
<td>0.632</td>
<td>0.46 (0.36–0.58)</td>
<td>21,553</td>
<td>24,12</td>
<td>2.57</td>
</tr>
<tr>
<td>TAC only</td>
<td></td>
<td>0.780</td>
<td>0.59 (0.50–0.70)</td>
<td>19,359</td>
<td>27,13</td>
<td>5.04</td>
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<tr>
<td>NTMR only</td>
<td></td>
<td>0.651</td>
<td>0.49 (0.37–0.65)</td>
<td>21,010</td>
<td>23,52</td>
<td>2.51</td>
</tr>
<tr>
<td>Local catastrophes ($\sigma_{cat} = 10$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TAC only</td>
<td></td>
<td>0.493</td>
<td>0.54 (0.49–0.60)</td>
<td>19,657</td>
<td>27,53</td>
<td>5.27</td>
</tr>
<tr>
<td>NTMR only</td>
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<td>0.382</td>
<td>0.45 (0.37–0.55)</td>
<td>20,887</td>
<td>23,20</td>
<td>2.52</td>
</tr>
<tr>
<td>TAC only</td>
<td></td>
<td>0.650</td>
<td>0.57 (0.50–0.64)</td>
<td>19,468</td>
<td>27,31</td>
<td>5.27</td>
</tr>
<tr>
<td>NTMR only</td>
<td></td>
<td>0.626</td>
<td>0.49 (0.38–0.61)</td>
<td>20,405</td>
<td>22,82</td>
<td>2.49</td>
</tr>
</tbody>
</table>

Notes: “Prob. N < 0.10N<sub>0</sub>” is the probability that the population has declined to less than 10% of the unfished population abundance. After an initial period of decline, an NTMR or TAC (producing equal population abundance after 100 time steps of simulation under deterministic conditions) was implemented, and subsequently simulations were run for 100 time steps. Abundance and yield (i.e., catch) are numbers of adult fish in the simulation; CPUE (catch per unit effort) is an index.
very low densities in areas outside the NTMR in time step 100 when the population was initially in decline (Fig. 3d). The same initial population managed with a lower TAC led to similar densities across all populations 100 time steps after the TAC was initially implemented (Fig. 3b). Spatial distribution after 100 time steps was similar for populations managed at $F_{MSY}$ with no NTMR (Fig. 3a) and populations initially in decline that were managed with TACs rather than an NTMR (Fig. 3b).

Implementation error

For a population initially in decline, the frequency histograms of abundance 20 time steps after the management strategies were first used were similar for populations managed using an NTMR and those managed using TACs when there were errors in the implementation of the TAC (Fig. 4b, d). However, the probability of falling below 10% of unfished abundance after 100 time steps was higher for TAC-based management (Table 2). This is in contrast to results obtained when the TAC was implemented without error in which the probability of falling below 10% of unfished abundance was lower for TAC-based management than for NTMR-based management (Fig. 2, Table 2). The probability of falling below 20% of unfished abundance over 20 or 100 years was greater for simulations with implementation error for a population managed at $F_{MSY}$ with no NTMR, but remained very low for a population with an NTMR and an optimal TAC (Table 3, Fig. 4).

Both interannual and inter-simulation variation in catch were greater under TAC management when the TAC was implemented with error. Interannual and inter-simulation variation in catch were higher when there was implementation error, irrespective of the management strategy applied (Tables 2 and 3; Appendix B: Tables B.1 and B.2).

**DISCUSSION**

Model results suggest that appropriate catch regulations are necessary for ensuring population viability in the presence of catastrophes, and that catch is always maximized with no NTMR. NTMRs combined with high TACs were associated with a higher probability of falling below 10% of the unfished adult abundance than management based only on TACs in the absence of implementation error, and irrespective of whether the catastrophes were local or global. In contrast, none of the management strategies led to a low probability of falling below 10% of unfished abundance for a population initially in decline when there was implementation error. In part, this reflects that the chosen
exploitation rate for the declining fishery was based on a rate that was well above $F_{\text{MSY}}$, leading to diffuse but low population densities in each area. In contrast, an NTMR used with appropriate catch regulations led to lower probabilities of falling below an abundance threshold, regardless of implementation error.

The spatial structure of population abundance created by these management strategies determined the ability of a population to survive catastrophes. Although an NTMR alone led to concentration of abundance within a small fraction of the available habitat (Fig. 3), conventional catch regulations led to distribution of abundance over the entire available range. A diffusely distributed population was more robust to catastrophes unless population abundance was already low (as for a fishery in decline managed using a TAC only) and error in the implementation of the TAC was high (Table 2, Fig. 4). Although spatial structure was important in determining the ability of management strategies to respond to catastrophes, the underlying mechanisms that caused the importance of spatial structure differed between local and global catastrophes.

### Local catastrophes

A spatially concentrated population is more susceptible to mortality from a local catastrophe than a population spread over a large range in the absence of implementation error; a local catastrophe with an epicenter near a spatially aggregated population (such as that created by an NTMR) led to additional mortality on essentially the whole population, whereas for a spatially diffuse population the same catastrophe would inflict this additional mortality on only a subset of individuals. Hence, in the absence of implementation error, a population in decline managed solely using an NTMR is more susceptible to local catastrophes than a spatially diffuse population (such as a population in decline managed solely with catch regulations). In contrast, a population managed using an NTMR in addition to optimal catch regulations is less susceptible to local catastrophes than a population managed optimally without an NTMR (regardless of implementation error) because spatial diffusivity is maintained and abundance grows within the NTMR such that a higher level of total abundance is achieved, acting as a buffer against falling below an abundance threshold.

### Global catastrophes

A concentrated population was more susceptible to global catastrophes than a diffuse population of equal abundance in our model. This counterintuitive outcome occurs because of the assumption of local density-
dependent mortality: the population builds nearly to local unfished abundance within the NTMR when there is an NTMR and high TACs; as local population size becomes large, larval survival decreases because mortality is density dependent, slowing the rate of population growth. With a lower TAC, densities are not high in any one area, so larval survival is higher and abundance can quickly rebuild in each area. Therefore, a diffuse population rebuilds more quickly after a catastrophe than a concentrated population and is likely to be more abundant in the event of a second catastrophe. This result will hold only if adults are sedentary; adult movement will lessen density within the reserve, causing increased larval survival (fewer deaths due to high density of larvae). In addition, this result may not hold if larvae do not disperse as a decreasing function of distance from a natal area (e.g., larvae pool and are redistributed evenly across areas) because the buildup of adults within an area would be fully decoupled from the density of larvae experiencing density-dependent mortality in that area. Furthermore, the incorporation of recruitment uncertainty is likely to change the frequency with which protected patches of populations reach density levels that are susceptible to significant density-dependent mortality.

In the optimally managed fishery, a global catastrophe that inflicts an additional fraction of mortality in each area will result in higher abundance if an NTMR exists (although a lower TAC would probably serve the same function). Higher abundance occurs because the initial abundance is greater as a result of the diffusely distributed abundance supplemented by a protected patch with high abundance.

Implementation error is a unique source of uncertainty because it applies only to fished areas. Therefore, implementing an NTMR will directly remove part of the population from this source of population fluctuation; this is why management of the declining fishery with TACs results in a higher probability of falling below 10% of unfished abundance and no longer outperforms an NTMR. The implementation error that we simulated was high; studies show that realized catch is typically

![Graph showing adult fish abundance](image-url)

**Fig. 3.** Adult fish abundance (mean, with dashed lines showing 5th and 95th percentiles) in time step 100 over space. Panels (a) and (c) show results for a population managed optimally (a) with TACs only and (c) with TACs in addition to an NTMR. Panels (b) and (d) show results for a population in decline prior to the implementation of (b) a lower TAC or (d) an NTMR. Catastrophes were global ($\sigma_{cat} = 50$ areas) with no temporal autocorrelation ($\rho = 0$); there was a high probability and magnitude of catastrophe ($\phi = \zeta = 0.288$), and no implementation error on TACs.
within 3–5% of specified catch limits in both overfished and well-regulated fisheries (Redstone Strategy Group and Environmental Defense 2007). Nevertheless, error still exists in estimates of population abundances and optimal fishing mortality rates, resulting in imperfect TACs.

A contrast to previous studies

Previous studies concluded or assumed that NTMRs increase population viability in the face of catastrophes and other uncertainties (Lauck et al. 1998, Mangel 2000, Rodwell and Roberts 2004, Halpern et al. 2006, Wagner et al. 2007). For example, Rodwell and Roberts (2004) simulated the implementation of an NTMR in declining fisheries with catastrophes and compared results to cases in which no management action is taken, finding that an NTMR increased population viability. This result was, however, not driven by the presence of catastrophes, but rather by the underlying (deterministic) structure of the model: several deterministic models have found that implementing a reserve in a fishery that is headed toward extinction will stabilize the population (e.g., Hilborn et al. 2006, McGilliard and Hilborn 2008). What Rodwell and Roberts (2004) do not include in their analysis is that although an NTMR implemented in a declining fishery is better than taking no action, catch regulations produce higher catch and CPUE as well as a lower risk of extinction than NTMRs.

Rodwell and Roberts (2004) also simulate a fishery in which NTMRs are implemented in addition to catch regulations; their results generally agree with ours: when catch regulations account for the presence of an NTMR, the NTMR may increase population viability in the event of catastrophes. Holland and Stokes (2006) find an equivalent result, but choose to focus on optimizing catch. As in our results, catch is always maximized with no NTMR.

Mangel (2000) includes catch fluctuations when evaluating the performance of NTMRs under multiple uncertainties, comparing population viability over a range of NTMR sizes from 0% to 100% of the area for a model without density-dependent mortality. In all simulations, a fishing mortality rate is applied such that the probability of population “success” (the percentage of simulations for which the population is above 35% of its unfished abundance) is 15%, a seemingly high fishing mortality rate that is similar in behavior to our fishery in decline. Mangel (2000) finds that population viability increases with increasing reserve size and makes the point, in common with other papers, that establishing an NTMR is more beneficial for population abundance than making no management changes, but proves this point under multiple uncertainties. We added to this work by comparing pairs of scenarios that exhibited similar model behavior under deterministic conditions (fisheries with optimal catches, with and without NTMRs; fisheries with NTMRs or TACs producing equal population abundances over time). Hence, we were able to distinguish the role of uncertainty from underlying deterministic model behavior. This allowed us to distinguish implementation error (catch fluctuations) as a unique source of uncertainty causing...
variation in catch, the effects of which are lessened by the presence of an NTMR. Our results agree with those of Mangel (2000) that NTMRs lower both catch and variation in catch in the presence of implementation uncertainty.

Potential for future work and conclusions

We assume that fish would be distributed evenly across areas in the absence of anthropogenic impacts, and hence do not account for natural sources of spatial heterogeneity in density. Many species may occupy different habitats in each life stage; some areas may serve as nursery grounds and older fish may reside in deeper waters (Berkeley et al. 2004, Gerber et al. 2005). Some hypothesize that recruitment may occur in distinct spatial patches, with most recruits in a given year originating from only one patch or a few patches (Berkeley et al. 2004). Especially in coral reef systems, it is thought that source–sink dynamics may occur, although empirical evidence of such dynamics is scarce (Crowder et al. 2000). Furthermore, tropical fish form short-lived spawning aggregations that are targeted by fishing fleets. Our conclusion that management outcomes reflect the ways in which regulations apply to spatially structured populations is an indication that any mechanism that structures a population in space can affect the vulnerability of stocks to catastrophes and the outcome of management strategies.

Introduction and spread of a disease is an example of a catastrophe that may exhibit characteristics that we did not model. For instance, the spread of disease depends on the density of the population; any mechanism that reduces the density of the population, such as fishing, may slow the rate of spread (McCallum et al. 2005). Likewise, a mechanism that increases the density of fish in a particular area, such as NTMRs, will speed the rate of disease spread (McCallum et al. 2005). Thus, there is a trade-off between fishing to decrease population density and perhaps reduce the spread of disease and regulating catch to prevent overfishing.

Future analyses should include multispecies interactions because the potential exists for changes in ecosystem trophic dynamics when managing spatially, using tools such as NTMRs (Micheli et al. 2004, Baskett et al. 2005, Martell et al. 2005). An NTMR will protect each species differently depending on relative rates of movement in and out of reserves, fishing mortalities, and trophic interactions.

We expanded on previous studies by showing that NTMRs are not always an insurance factor against falling below population thresholds due to catastrophes, as is commonly assumed. We showed that the spatial structure of populations is the key variable in determining response to catastrophes. NTMRs change the spatial structure of populations, therefore affecting the ability of populations to remain extant under highly variable conditions.


**APPENDIX A**

Equations for population and fishery dynamics (Ecological Archives A021-065-A1).

**APPENDIX B**

Non-catastrophic mortality, inter-simulation CV of catch and CPUE in year 100 (Ecological Archives A021-065-A2).