Catastrophic Mortality, Allee Effects, and Marine Protected Areas

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Submitted December 8, 2017; Accepted September 8, 2018; Electronically published February 1, 2019

Online enhancements: appendixes.

Abstract: For many species, reproductive failure may occur if abundance drops below critical Allee thresholds for successful breeding, in some cases impeding recovery. At the same time, extreme environmental events can cause catastrophic collapse in otherwise healthy populations. Understanding what natural processes and management strategies may allow for persistence and recovery of natural populations is critical in the face of expected climate change scenarios of increased environmental variability. Using a spatially explicit continuous-size fishery model with stochastic dispersal parameterized for abalone—a harvested species with sedentary adults and a dispersing larval phase—we investigated whether the establishment of a system of marine protected areas (MPAs) can prevent population collapse, compared with nonspatial management when populations are affected by mass mortality from environmental shocks and subject to Allee effects. We found that MPA networks dramatically reduced the risk of collapse following catastrophic events (75–90% mortality), while populations often continued to decline in the absence of spatial protection. Similar resilience could be achieved by closing the fishery immediately following mass mortalities but would necessitate long periods without catch and therefore economic income. For species with Allee effects, the use of protected areas can ensure persistence following mass mortality events while maintaining ecosystem services during the recovery period.

Keywords: catastrophe, marine reserves, fishery management, marine protected area (MPA), abalone, recruitment failure, resilience, marine populations, environmental shocks.

Introduction

Understanding, quantifying, and improving resilience of wild populations to natural and anthropogenic disturbance is a central problem in ecology, conservation biology, and natural resource management (Dunham et al. 1999; Levin and Lubchenco 2008). Defaunation in the Anthropocene has been extensively documented in both terrestrial (Dirzo et al. 2014) and marine (McCauley et al. 2015) environments as a consequence of land-use change, pollution, and overharvesting. For species that experience Allee effects—that is, lower breeding success at low densities (Allee 1932)—a period of heightened mortality can reduce abundance to a level that threatens recovery (Gascoinne and Lipcius 2004). The most dramatic consequence of Allee effects is the negative per capita population growth when a population drops below a critical density threshold, further lowering abundance and growth in a negative feedback loop or “extinction vortex” (Gilpin and Soulé 1986; Fagan and Holmes 2005). This risk is exacerbated for harvested species and, in particular, fisheries, as exploited populations are typically maintained at artificially low densities even when carefully managed to guarantee long-term, maximum sustainable yield (MSY). The combination of natural environmental variability and anthropogenic pressure increases the likelihood that harvested populations drop below the density at which breeding success diminishes, making such species particularly vulnerable to Allee effects (Berec et al. 2007). In addition to slowing or preventing recovery in exploited species, Allee effects increase uncertainty and may amplify the effects of demographic stochasticity, environmental variability, and harvest-induced cycling (Fryxell et al. 2010; Kuparinen et al. 2014). The risk of reproductive failure in exploited populations may further increase when harvesting specifically targets population aggregations (Sadovy and Domeier 2005), males (Petersen and Levitan 2001), or large spawners (De Leo and Micheli 2015).

A drop in fertilization success at low population density has been extensively documented in marine environments for broadcast spawners and observed in several harvested benthic invertebrates, including queen conch (Stoner et al. 2014), sea urchin (Levitan et al. 1992), and abalone (Babcock et al. 1999; Hobday et al. 2000). Other marine examples characterized by Allee effect at low population density include...
vertebrates such as herring (Saha et al. 2013), cod, and pollock (Keith and Hutchings 2012). Terrestrial examples of harvested species that experience Allee effects are rarer than in the ocean but include elephants (Dobson and Poole 1998) and plants such as wild ginseng (Hackney and McGraw 2008). Maintaining viable breeding densities for such species is a challenge, as the collapse for exploited species is often plateau shaped, meaning that it may occur suddenly without early-warning signals of decline (Mullon et al. 2005; Boetti and Hastings 2013), and is therefore difficult to anticipate. Incorporating Allee effects into management and bio-economic models is thus critical to long-term sustainability (Lande et al. 1994, 1995), especially for exploited populations divided across multiple populations (Stephens and Sutherland 1999; Frank and Brickman 2000) or subject to high environmental variability (Fryxell et al. 2010).

As anthropogenic warming intensifies, many ecosystems are experiencing gradual yet inexorable environmental change. In marine ecosystems, increased temperature, acidification, deoxygenation, and disrupted hydrodynamic and productivity patterns are shifting species ranges and altering their life histories (Walther et al. 2002; Parmesan and Yohe 2003; Perry et al. 2005; Harley et al. 2006; Fabry et al. 2008; Cheung et al. 2009; Hoegh-Guldberg and Bruno 2010; Donnelly et al. 2012). In addition to long-term trends, climate change can also increase the likelihood of extreme environmental events and sudden shifts (Jentsch et al. 2007; Hegerl et al. 2011). Many marine species are threatened by prolonged temperature spikes (e.g., Dayton and Tegner 1984; Garehabou et al. 2009; Wernberg et al. 2013), including major impacts of the 2015–2016 El Niño on coral reefs (Normile 2016). Higher temperatures and altered upwelling patterns contribute to a greater incidence of hypoxia and associated mass mortality (Diaz 2001; Grantham et al. 2004; Chan et al. 2008; Vaquer-Sunyer and Duarte 2008). These “catastrophes,” which typically involve high proportional mortality applied broadly across the population, can be difficult to predict and integrate into sustainable management (Wagon et al. 2007; Game et al. 2008; Gepart et al. 2017). Species with low mobility and reduced reproductive success at low density—that is, those experiencing Allee effects—are particularly vulnerable to mass mortality events. Sessile individuals, such as coral and oysters, or those unable to quickly move to avoid a local environmental extreme, such as many sedentary benthic invertebrates and fish, cannot relocate to avoid stressful high-temperature or low-oxygen conditions.

One strategy for maintaining a fishery managed at MSY after an unexpected mass mortality event is to close it as long as necessary to allow the population to recover. However, if population density at MSY was already close to the Allee threshold, a catastrophic event may push it below the minimum density for recovery, and the population may collapse and fail to recover despite a complete cessation of fishing (Hutchings and Reynolds 2004). Even when recovery is possible, fishing closure may be economically and socially unsustainable if recovery is slow and requires a prolonged multiyear closure, causing a significant loss of catch and income and, ultimately, the possible collapse of the entire business sector (e.g., sardines in Monterey [Radovich 1982] and cod in Newfoundland [Myers et al. 1997]). Alternatively, the fishery can be managed by setting harvesting effort below that at MSY, decreasing fishing mortality and maintaining population well above the Allee threshold density as a buffer against unexpected loss (the precautionary principle; Lauck et al. 1998). If catastrophes are infrequent, however, this approach would produce suboptimal catch most years. Instead, managers could use a network of marine protected areas (MPAs), including fully no-take reserves, to maintain high-density regions while fishing at MSY levels elsewhere (De Leo and Micheli 2015). After a catastrophe, larval dispersal from the successfully breeding MPAs can bolster recruitment in neighboring low-density regions where recruitment failure may occur, protecting against the Allee effect (Quinn et al. 1993; Shepherd and Brown 1993; Allison et al. 2003). Although prior work has considered the effectiveness of reserves as a buffer against environmental uncertainty (Mangel 2000; Halpern et al. 2006), catastrophes (Allison et al. 2003; McGilliard et al. 2011), or Allee effects (Quinn et al. 1993) separately, here we explore, for the first time, how effective a range of management strategies are in maintaining a harvested species that experiences high environmental variability and catastrophic events and whose dynamics at low density are characterized by the Allee effect.

In this study, we investigated whether the use of spatial management via a system of no-take zones can protect a sedentary species with Allee-driven recruitment failure from extinction during catastrophic mortality events and, possibly, speed postcatastrophe recovery of abundance and catch compared with nonspatial management. We used the green abalone (Haliotis fulgens) fishery at Isla Natividad, in Baja California Sur, Mexico (Rossetto et al. 2015), as our reference case. Abalone (Haliotis spp.) are broadcast spawners and have been shown to have low recruitment success when their abundance is low (Babcock and Keesing 1999; Rogers-Bennett et al. 2004; Blaauw 2013; Catton and Rogers-Bennett 2013). In the US state of California, they have been heavily impacted by fishing for decades, with many populations at less than 1% of their unflushed abundance (Rogers-Bennett et al. 2002). There is ample evidence that abalone populations experience sudden mass mortality events. For some species—for example, the black abalone (H. cracherodii)—outbreaks of withering syndrome have caused rapid and extreme decline in southern California (Lafferty and Kuris 1993). Mexican fisheries have been strictly managed over the past decades, after populations were reduced by excessive fishing and extreme El Niño–Southern Oscillation events (Shepherd et al. 1998;
Morales-Bojórquez et al. (2008). More recently, prolonged hypoxic events have caused mass abalone die-offs of 50%–75% at Isla Natividad (Micheli et al. 2012). However, the voluntary no-take marine reserves established and enforced by the fishing cooperative of Isla Natividad maintained higher postcatastrophe density (due to the removal of all fishing-associated mortality in the reserves) and significantly larger abalone sizes compared with the fished regions, with correspondingly higher recruitment and larval spillover across the reserve boundaries, indicating that reserves can support the resilience of impacted populations (Micheli et al. 2012).

Previous models of abalone populations from Isla Natividad and southern California have concluded that recovery times after extreme depletion can be long (decades) but that networks of small reserves decrease the risk of extinction and buffer populations against management errors, such as setting quotas that are too high (Catton and Rogers-Bennett 2013; Rossetto et al. 2015). However, despite robust evidence of Allee effects in abalone recruitment, previous work on the effects of MPAs on abalone recovery did not account for the risk of recruitment failure following mass mortality events. McGilliard et al. (2011) assessed recovery with MPAs after mild catastrophes but did not include any form of negative density dependence (i.e., decrease in recruitment at low densities). Rossetto et al. (2015) simulated fishery recovery from overexploitation without considering depensation or regional mass mortality. Here, we address these critical biological and environmental processes—Allee effects and environmental shocks—and their possible influences on future persistence of abalone populations and fisheries and, by extension, marine species with similar life-history characteristics, via a modeling framework that is generally applicable to broadcast-spawning benthic invertebrates.

Our model builds on the spatially explicit stage-structured model developed by Rossetto et al. (2013, 2015) to study marine reserve impact on abalone population persistence and fishery production. Because abalone fecundity and survival, as in many marine invertebrates, are sensitive to small changes in size (Rossetto et al. 2012, 2013), we extended the original modeling framework based on arbitrary size classes and developed a novel integral projection model (IPM; Ellner and Rees 2006), allowing continuous size structure. Following Catton and Rogers-Bennett (2013), we added an Allee effect producing diminished fertilization success at low adult density. Using this model, we analyzed postcatastrophe (defined here as >50% mortality) recovery under three realistic constant-effort management strategies: no closure, temporary fishery closures, and no closure with portions of the coastline designated as no-take reserves. All of these strategies are used to manage coastal fisheries in Baja California (McCay et al. 2014) and around the world. We explored how catastrophe severity and frequency, Allee strength, and carrying capacity affect fishery outcomes. For each scenario, we determined the likelihood of fishery collapse and calculated mean catch and proportion recovered after 20 years (the typical length of the abalone concession granted to fishing cooperatives in Mexico; McCay et al. 2014).

Material and Methods

Model Description

We used a spatially explicit IPM (Ellner and Rees 2006) to simulate recruitment, survival, and growth of green abalone (Haliotis fulgens) within a continuous size structure. All model parameters and equations are given in appendix A. We used a probabilistic nonnegative growth function (Bardos 2005) to model annual abalone growth (fig. 1A). This growth model was developed to accommodate the strongly variable growth dynamics of abalone as seen in field data from Troyinkov et al. (1998) and to model population dynamics using length alone rather than size-at-age conversion. Abalone survival in natural environments increases linearly with body mass, which can be estimated from length (fig. 1B; Rossetto et al. 2012). Similarly, egg production for mature adults increases exponentially with length (fig. 1C; Tutschulte 1976).

Following Button’s (2008) empirical study, we modeled the Allee effect by assuming that breeding success is an increasing and saturating function of spawner density that levels off to 1 at high density and tends to 0 at low density (fig. 1D). The threshold density below which recruitment begins to fail determines the strength of the Allee effect and affects the chance of population recovery after a mass mortality event. Although recent studies have emphasized the importance of Allee effects for conservation (Courchamp et al. 1999; Stephens and Sutherland 1999), it is still unclear how broadly applicable they are to marine species. Myers et al. (1995) found evidence of recruitment failure due to low population density in a few fisheries, but the signal can be hard to discern (Liermann and Hilborn 1997, 2001) and recent meta-analyses found little evidence across a wide range of taxa (Hilborn et al. 2014). However, Tegner (1993) found that isolated abalone populations were unable to recover following a fishery closure until recruitment was augmented by larval dispersal from nearby transplants, suggesting that Allee effects are potentially important to sedentary invertebrates. The assumption of the existence of an Allee effect in the stock being managed is critical to the applicability of our model. Given the harvest assumptions, postcatastrophe recovery is guaranteed if there is no threshold below which recruitment begins to fail. In accordance with Button (2008), we set the threshold density below which breeding success begins to drop to ∼0.2 abalone/m2 and, to account for the uncertainty in the estimation of this threshold, we tested sensitivity to the strength of the Allee effect, including its absence, in appendix C (apps. B, C are available online).
We modeled the coastline of Isla Natividad as a circular set of 150 blocks measuring 100 m (alongshore) by 500 m (offshore; distance based on fishable habitat as determined by Rossetto et al. [2015]) and containing subpopulations connected via stochastic larval dispersal (fig. 2A). We assumed that larvae dispersed in a Gaussian fashion with a mean dispersal distance that, based on field observations (Micheli et al. 2012), varies stochastically from year to year according to a gamma distribution (modal distance of 300 m from field data; fig. 2B). We further assumed a closed system, with offshore larval input or loss assumed to be compensatory with no net effect on local recruitment and annual fluctuations in relative settler survival rate due to year-to-year environmental variability (fig. 2C; Szuwalski et al. 2015). We assumed density-dependent settlement and set the per-patch carrying capacity to produce an unharvested density of \( \sim 0.2 \) ind./m\(^2\), based on the work of McShane (1991) and Daume et al. (2004) and consistent with field observations (Rogers-Bennett et al. 2004; Micheli et al. 2008). We assumed homogeneous habitat both within and between patches.

We modeled catch as a constant proportion \( h \) of commercial-size abalone harvested from each fishable patch annually, representing a constant level of effort. For the non-spatial management strategies, we set \( h_{\text{NC}} \) to 2/3 of the fishing pressure producing MSY (\( F_{\text{MSY}} \)), as determined by prior simulation without catastrophes (app. B). This is the standard precautionary reference point typically used in fisheries management (Jennings et al. 2001) to offset errors in parameter estimation and uncertainties in stock assessment and population dynamics. It is generally considered a good compromise between maximizing sustainable yields and minimizing risk of collapse. The harvest rate in the fishable ground under the MPA strategy was set so that the spatial mean of the harvesting rate along the entire coastline (including the protected areas where \( h = 0 \)) was equal to that under the no-closure strategy, that is, \( h_{\text{MPA}} = h_{\text{NC}}/(1 - \text{fpc}) \), where fpc is the overall fraction of protected coastline and \( h_{\text{NC}} = 2/3F_{\text{MSY}} \).

### Analysis of Management Strategies and Catastrophe Scenarios

Conventional management without reserves was simulated as constant harvest pressure \( h_{\text{NC}} \) with either no interruption (the no-closure or NC strategy) or a moratorium on harvest...
after the catastrophe until stock had recovered to >50% of precatastrophe density (the dynamic-closure or DC strategy). We set the reopening threshold for the DC strategy as the point at which catch is maximized without substantially decreasing the likelihood of recovery in the default scenario (app. C; fig. C2B; figs. B1, C1–C3 are available online). The NC and DC strategies had no area set aside as reserves, while 20% of the fishing ground was protected under the MPA strategy with six 500-m reserves (the optimal size derived from Rossetto et al. [2015] and our own sensitivity analysis; see app. C and fig. C3B). We conducted a sensitivity analysis of model outcomes with respect to (i) the fraction of fishing ground under protection (ranging from 10% to 80%), (ii) the size of each MPA (1, 2, 5, 10, and 15 km), and (iii) dispersal distance (from 25% to 200% of the default dispersal distance, with a 25% increment for each scenario). Harvest rate in the fished patches under the MPA strategy was kept constant (i.e., no fishing closure) for the entire simulation time. For each management strategy, we ran the model with the respective fishing pressure ($h_{\text{NC}}$ for NC and DC and $h_{\text{MPA}}$ for the MPA strategy) until an equilibrium was reached and then applied a global catastrophic event causing 75% mortality to all age classes (the “severe” catastrophe scenario). We then ran the model for an additional 150 years and assessed whether the population recovered or collapsed (remained below 10% of precatastrophe maximum catch at the end of the simulation; Worm et al. 2006; Costello et al. 2008). We repeated the simulation 1,000 times and calculated two metrics: the proportion recovered (i.e., the proportion of simulations in which catch recovered above the 10% threshold) and the 20-year catch (i.e., the total present-day value of catch over the 20 years following the catastrophe, discounted 5% annually).

We ran a sensitivity analysis of model outcomes with respect to the severity of the catastrophic event (ranging from moderate [i.e., 50%] to extreme [i.e., 90%] mortality) and compared the baseline scenario (one moderate catastrophic event causing 75% mortality) with multiple-catastrophe scenarios (two moderate catastrophes 15, 10, or 5 years apart and three moderate catastrophes 5 years apart). As there is considerable uncertainty about abalone carrying capacity—that is, the unfished population density—we also analyzed the performance of management scenarios under alternative assumptions of the precatastrophe population density ranging from low (∼0.06 ind./m² for the NC strategy at 60% of baseline, unfished carrying capacity) to high (∼0.25 ind./m² at 200%). Because we assumed that precatastrophe management was sustainable and error-free, we adjusted harvest pressure to match the $F_{\text{MSY}}$ for each density (app. B).

The results from additional scenarios and sensitivity analyses are given in appendix C. All simulations were run using the programming language R (ver. 3.2.1; R Development Core Team 2012).
Results

For the baseline scenario, the combination of Allee effect and the catastrophe increased the likelihood of collapse of a fishery that would be otherwise sustainable in the absence of extreme environmental conditions (fig. 3A). Because the decline of breeding success is nonlinear (fig. 1D), fishery collapse occurred as a threshold effect from the intersection of three factors: precatastrophe equilibrium density, strength of the Allee effect, and severity of the catastrophe. The Allee effect intensified further when population density was below \(\sim 0.2 \text{ ind./m}^2\), the carrying capacity in the baseline scenario. Catastrophe severity (figs. 4, 5) and precatastrophe density (fig. 6) determined how far the population dropped below the Allee threshold. The ability of a harvested subpopulation to recover depended on a combination of factors, including (i) local replenishment (i.e., postcatastrophe density), (ii) whether fishing activities are halted after a catastrophic event or not (NC vs. DC strategies), and/or (iii) larval input from high-density regions (NC vs. MPA strategies; fig. 3).

Our simulation showed that the presence of MPAs was able to avoid fishery collapse after a catastrophe in cases where uninterrupted harvest with fishing effort at precatastrophe levels would prevent recovery (figs. 3, 4). Under the no-closure (NC) management strategy, the likelihood of recovery dropped quickly with increasing catastrophe strength, with only 56% of simulation runs recovering after a severe catastrophe and 0.1% after an extreme one (fig. 4A, diamonds). Implementing a dynamic postcatastrophe fishery closure (the DC strategy) decreased the risk of collapse to 1.7% for the baseline scenario.

**Figure 3:** Time series for baseline model with three management strategies. The first and second columns correspond to the constant effort model without and with a dynamic postcatastrophe harvest moratorium, and the third column shows results for the 20% marine protected area (MPA) network. Horizontal axes indicate time, with a severe catastrophe (75% mortality) occurring at \(t = 150\). Vertical axes indicate abalone adult density for the first two rows and cumulative catch in metric tons for the third row. Solid lines show mean density within fished regions for recovering populations, dashed lines show mean density within reserves, and dotted lines show mean density for collapsing fisheries. A–C, Full management-specific time series of stock density. Percentage indicates the fraction of 100 simulation runs that collapsed. D–F, Close-up of the 50-year postcatastrophe recovery period. G–I, Cumulative postcatastrophe catch in the 50-year postcatastrophe recovery period.
(fig. 4A, dashed line) and to 39% for extreme catastrophes (fig. 4A, circles), but at the cost of greatly reducing catch due to closure times in excess of 10 years (fig. 4B). However, establishment of an MPA network (the MPA strategy) dropped the risk of collapse to 0%–0.1% for moderate to severe catastrophes and to substantially less than that for the NC strategy for higher severity catastrophes (fig. 4A, triangles). Catch for the MPA strategy was ~73%–89% that of the NC strategy, depending on the scenario (fig. 4).

When multiple moderate catastrophes (50% mortality) occurred during the simulation time, the DC strategy protected the fishery from collapse only marginally better than the NC strategy in most scenarios, and the MPA strategy was superior to both nonspatial strategies, reducing the proportion collapsed to almost zero for all dual-catastrophe scenarios (fig. 5A). The 20-year catch was similar between the three strategies but was lower for the DC strategy because of long mean closure times (10–30 years; fig. 5B), which reduced the harvest.

For a given catastrophe severity, the degree to which postcatastrophe population density is below the Allee threshold depends on precatastrophe density. With high carrying capacity (~0.4 ind./m²), there is little likelihood of collapse following a severe catastrophe regardless of management strategy (fig. 6A, upper right). As carrying capacity decreases, the probability of recovery decreases rapidly for the NC strategy and gradually for the DC and MPA strategies but remains higher for the DC strategy for more severe catastrophes (fig. 6A). As for the other scenarios, catch was substantially lower for the DC strategy because of long mean closure times (10–30 years; fig. 6B).

These results suggest that MPA networks are more effective than constant MSY-based fisheries management in mitigating the risk of fishery collapse following a mass mortality event. When compared with the use of dynamic fisheries closures, moreover, the MPA strategy provided recovery likelihoods almost as high for moderate to severe catastrophes while maintaining high catch due to no fishery closure. After a severe catastrophe (fig. 4A, dashed line scenario), for example, the MPA strategy reduced the likelihood of collapse to near zero, similar to the DC strategy, but catch was 142% higher than that of the DC strategy. For more extreme catastrophes, the MPA strategy had substantially lower recovery likelihood, but 20-year catch for the DC strategy was near zero due to long closures (fig. 4A, 4B). The higher precatastrophe

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**Figure 4:** A. Catch and population recovery proportion for each management strategy under varying catastrophe severity. The vertical axis indicates the proportion recovered, that is, the proportion of simulation runs that recovered following the catastrophe. The horizontal axis indicates the 20-year catch, that is, the mean cumulative catch over the 20-year postcatastrophe period. Catch was discounted 5% annually, and only noncollapsing simulation runs were included. The contours link the three management strategy outcomes for each catastrophe scenario. Catastrophe severity ranges from moderate (50% mortality) in the upper right to extreme (90% mortality) in the lower left, increasing by 5% increments. The baseline scenario (75% mortality) is indicated by a dashed contour line. B. Mean length of fishery closure for the dynamic-closure model. The horizontal axis indicates catastrophe severity, and the vertical axis shows mean length of closure. Error bars show 1 SD. MPA = marine protected area.
population density within the reserve translated to higher post-catastrophe density and allowed larval dispersal from the reserves to rescue the fished regions negatively impacted by the Allee effect. In the case of multiple moderate catastrophes, this dynamic made the MPA strategy clearly superior to the DC strategy (fig. 5A).

As shown above, increased severity of catastrophe and lower precatastrophe population density both increased the likelihood of collapse and slowed down recovery. In appendix C, we explore the sensitivity of model results to other factors. Both an Allee effect stronger than the default empirically estimated following Button (2008; i.e., higher sensitivity of aggregation size to density; fig. C1) and greater mean larval dispersal distance (fig. C3C) increased the risk of catastrophic collapse of the fishery. Greater larval dispersal sped up recovery in the fished areas due to higher larval spillover, but the lower larval retention resulted in lower equilibrium density within the MPAs and thus a smaller buffer against catastrophes. For the nonspatial strategies, a decrease in proportion of $P_{\text{MSY}}$ decreased both catch and the chance of collapse (fig. C2A), with a similar trend for the reopening threshold for the DC strategy (fig. C2B).

Discussion

In recent decades, climate change and the increased frequency of extreme events such as droughts, floods, heat waves, and—specific to aquatic environments—prolonged hypoxia have added additional burden to the many anthropogenic stressors that threaten the persistence of natural populations of conservation and commercial interest. Mass mortality events can reduce a population to unexpectedly low densities, exceeding the variability factored into standard “ecological stability” management models (Roughgarden and Smith 1996). The effects of low population density extend beyond recruitment failure, with implications for behavior, predator interaction, environmental modification, patch choice, and more (Stephens and Sutherland 1999).

Risk of local extinction is greatly exacerbated when relevant fitness/demographic parameters, such as fertilization rate, fecundity, and/or survival, decrease in sparse, low-density populations. For wild populations that experience Allee effects, it is thus crucial to understand how to avoid the “extinction vortex” and improve resilience to mass mortality events by acting on the spatial and temporal distribution of those anthropogenic stressors that can be directly managed. While the Allee effect is a central concept in ecol-

Figure 5: A, Catch and population recovery proportion for each management strategy under varying catastrophe number and frequency. The axes are as described in figure 4A. The scenarios are as follows: one moderate (50% mortality) catastrophe (solid line), two moderate catastrophes 15 years apart (dashed-dotted line), two moderate catastrophes 10 years apart (long-dashed line), two moderate catastrophes 5 years apart (short-dashed line), and three moderate catastrophes 5 years apart (dotted line). B, Mean length of fishery closure for the dynamic-closure model. Same as for figure 4B, except that the horizontal axis shows the five catastrophe categories described above. MPA = marine protected area.
ogy and conservation biology, most quantitative studies have focused on viability assessment for spatially homogenous populations (e.g., Ortigosa et al. 2000) or are in the context of meta-population frameworks (Amarasekare 1998; Kuussaari et al. 1998; Brassil 2001). In this work, we investigated the interaction among (i) large-scale mass mortality events, (ii) fine-scale distribution of anthropogenic disturbance in the form of fishery mortality, and (iii) recruitment dispersal on a spatially explicit coastal habitat for populations with Allee effects and explored how alternative configurations of spatial and temporal reduction in anthropogenic disturbance can increase the resilience of populations subject to increased frequency and intensity of extreme events. We developed the analysis with specific reference to marine populations of broadcast spawners, for which Allee effects have been clearly documented and whose persistence is relevant for their ecological and conservation value as well as for the ecosystem services they deliver in terms of seafood production in coastal fisheries.

Our model predicts that a network of protected areas that reduce or possibly eliminate anthropogenic disturbance can minimize the risk of population collapse caused by large-scale extreme climatic events for species whose dynamics at low density are characterized by an Allee effect. Networks of protected areas can effectively increase resilience if their size and spatial layout are able to maintain a breeding population sufficient to rebuild the reproductive potential despite the presence of Allee effects (Allison et al. 2003; Wanger et al. 2007; Game et al. 2008). Our results are consistent with the general finding that management using protected areas provides a buffer against uncertainty, which in fisheries reduces catch variability and smooths the effects of recruitment stochasticity (Lauck et al. 1998; Mangel 2000; Rodwell and Roberts 2004; Halpern et al. 2006; Pitchford et al. 2007; West et al. 2009; Barnett and Baskett 2015). Species with Allee effects are particularly sensitive to negative secondary effects from anthropogenic disturbance, such as fishing mortality (Petersen and Levitan 2001; Fryxell et al. 2010), with increased uncertainty of recovery (Kuparinen et al. 2014), and our results confirm that spatial management can mitigate this vulnerability. Although occasional cessation of harvest can be used in a nonspatial strategy to avoid dropping below an Allee threshold (e.g., Kar and Matsuda 2007), such a management strategy might not be sufficient in the case of strong and unpredictable external sources of mortality and increasing frequency of extreme and catastrophic events.

Figure 6: A. Catch and population recovery likelihood for each management strategy under varying carrying capacity. The axes are as described in figure 4A. Carrying capacity ranges from high (0.4 ind./m², or 200% of baseline carrying capacity K) in the upper right to low (0.1 ind./m², or 50% of K) in the lower left, decreasing by increments of 10% of K. The baseline scenario (0.2 ind./m²) is indicated by a dashed contour line. Note that because harvest proportion h is set dynamically for each scenario, proportional change in precatastrophe population density does not exactly match proportional change in K. B. Mean length of fishery closure for the dynamic-closure model. Same as for figure 4B, except that the horizontal axis indicates relative precatastrophe density. MPA = marine protected area.
McGilliard et al. (2011) predicted that for sustainably managed fishery stocks, as with our model, MPAs in combination with fishing mortality reduction (i.e., catch limitation) would greatly decrease the likelihood of catastrophe-induced population collapse compared with catch regulation alone. For harvested populations already in decline, however, strict catch limitations alone were superior, according to McGilliard et al. (2011), to MPA establishment without fishing reduction unless the model included substantial errors in catch assessment. There are four key differences between our modeling analysis and that of McGilliard et al. (2011) that might explain this discrepancy. First, their model had a single MPA (in contrast to an optimal network of MPAs), thus minimizing the potential positive effects of larval spillover. Second, the catastrophes considered by McGilliard et al. (2011) were significantly less severe than those simulated with our model. Third, their model did not include size structure, eliminating the recruitment benefits gained from protecting large old spawners within MPAs. Fourth and most important, their population model had no negative density-dependent effects in recruitment, so it did not account for the risk of recruitment failure when population density in fished areas dropped below the Allee threshold.

The impact on ecosystem services, especially seafood production, of conservation strategies aimed at increasing the resilience of population to extreme climatic events should also be accounted for, as it might also have a positive effect on the short-term social acceptability of alternative conservation schemes. Our analysis shows that spatial management through a network of protected areas may come at the cost of a decrease in total catch with MPAs depending on scenario, both pre- and postcatastrophe, compensated by a dramatic drop in the chance of fishery collapse. The value of this trade-off depends on the expected frequency and severity of catastrophes and how likely the population is to experience reproductive failure following a sudden drop in abundance. Booth et al. (2014) showed a 15-year decreasing trend in dissolved oxygen in southern California, for example, which may lead to more frequent extreme hypoxia events. For slow-growing species, an economically viable 5–10-year fishery closure is likely insufficient to guarantee recovery from a severe decline below the Allee threshold and therefore extended protection in MPAs is more effective, whereas short-term closures may be preferable for fast-growing species (e.g., Cudney-Bueno et al. 2009). Even when catastrophes are expected to be rare and moderate, the uninterrupted annual income that the MPA management approach allows may be preferable for fishers to a lengthy fishery closure. While an individual fisher may be able to tolerate a fishing closure as long as 5 years, a fishing moratorium lasting 10 or 15 years out of a 20-year concession would likely be financially unsustainable.

Coastal fisheries of Baja California are managed by fishing cooperatives that were granted exclusive access rights to abalone, lobster, and other marine invertebrates and algae beginning in the 1930s (McCay et al. 2014). At Isla Natividad and other locations in this region, MPAs were voluntarily established and enforced by the fishing cooperatives, which conduct surveillance of their fishing grounds and of the reserves. Thus, poaching and noncompliance with no-take regulations are minimal (Micheli et al. 2012). In other regions, local closures can face significant opposition, and noncompliance and poaching can negate the potential benefits of closures (Edgar et al. 2014). Displaced fishing effort may exert negative impacts on populations and habitat outside reserves or leave the industry rather than relocating, increasing the catch “penalty” of the MPA strategy (Hilborn et al. 2004; Abbott and Haynie 2012). For abalone, spillover from the MPA occurs via larval dispersal, but for a fishery with mobile, harvestable adults, reallocated effort along the MPA boundary (e.g., Murawski et al. 2005; Stelzenmüller et al. 2008) can potentially reduce overall catch (Kellner et al. 2007) and may hinder postcatastrophe recovery.

Another potential challenge is an increase in harvest as a species becomes rare due to increasing prices (the anthropogenic Allee effect; Courchamp et al. 2006; Hall et al. 2008). In the case of green abalone at Isla Natividad, prices are set by the global market and are not affected by local abundance, but for some species (such as, in the past, white abalone in California; Davis et al. 1998) the increase in illegal harvest can disrupt management efforts. Aquaculture is a potential outlet for displaced fishing effort, especially in response to rising global seafood demand, and has been successful for some abalone species (Searcy-Bernal et al. 2010). However, aquaculture operations are also at risk from extreme events that can impact aquaculture infrastructure and species through storms, harmful algal blooms, acidification, and hypoxia. The possible role of aquaculture in contributing to seafood production and income in small-scale fisheries in the face of environmental variability and extremes remains to be addressed.

Disease outbreaks, an increasing source of mass mortality in marine systems (Harvell et al. 2004), represent a particular challenge for marine reserves (McCallum et al. 2005; Wootton et al. 2012). If disease transmission increases with density, the impact of outbreaks may be intensified within MPAs, diminishing their effectiveness (McCallum et al. 2005). However, our model focused on low densities near the Allee threshold for which we do not expect disease dynamics to be strong, particularly during the immediate postcatastrophe period. Additionally, some diseases have a strong environmental trigger (e.g., abalone withering syndrome; Ben-Horin et al. 2013) and may produce mass mortality events with little density-dependent transmission. Last, as McCallum et al. (2005) demonstrate, the presence of pathogens can decrease reserve performance only down to that of conventional management, not below. Consequently, we expect our results to apply broadly even in the presence of disease outbreaks.
As with all simulations, our model makes a number of simplifying assumptions to reduce computational complexity and produce a more general outcome. On the basis of Button (2008), we assume a simple nonlinear shape to the Allee effect, with a rapid decrease in breeding success starting at roughly 0.2 ind./m². While this is consistent with prior experimental work and field observations, density is a proxy only for aggregation size and calculations based on observed density during field surveys may overestimate the Allee effect (Lundquist and Botsford 2011). Abalone may aggregate in larger groups during spawning, allowing successful fertilization even at low densities (Micheli et al. 2008, 2012; but see Coates et al. 2013). A more linear decline in breeding success would also diminish the power of the Allee effect, as is suggested by theoretical models of aggregation and sperm dispersal (Lundquist and Botsford 2004), which would potentially eliminate the recovery advantages of the MPA strategy (app. C; fig. C1A). Our model does not include demographic stochasticity, but we would not expect any significant effect until densities were much lower than those seen here (the default Allee threshold of 0.2 ind./m² is equivalent to 10,000 individuals per block). The Gompertz growth function we use in this model assumes nonnegative growth of abalone shell, even though reduction of abalone condition has been observed in some cases (Button and Rogers-Bennett 2011) and did not provide the best fit for abalone growth data in some prior studies (Rogers-Bennett et al. 2007).

Our model used a simple homogenous spatial structure that ignores potentially important factors, such as spatial heterogeneities in local productivity, fishing pressure, and larval dispersal. Catastrophes such as extreme hypoxia are unlikely to be global in scale (affecting optimal MPA placement; Wagner et al. 2007) or, additionally, to produce size-independent mortality. Clark et al. (2013) found that, for clams, large mature adults were the most vulnerable to hypoxia, which, if true of abalone, would potentially decrease the postcatastrophe fecundity of the MPAs and thus their ability to buffer against collapse. Finally, genetic data from Isla Natividad suggest that, while there is measurable gene flow from external sources, there is insufficient input of larvae to create a “rescue effect” when local populations are low (Munguía-Vega et al. 2015). Consequently, we believe that the year-to-year variability in recruitment success, as implemented in our model, provides sufficient stochasticity to implicitly account for moderate rescue effects from larval supplement from exogenous sources as well as fluctuating environmental conditions. We expect the recovery benefits of the MPA strategy to be greatest for a fishery with infrequent pulses of larvae or older individuals from external sources.

Finally, we have assumed a homogenous habitat, symmetric larval dispersal, and simplified bioeconomic conditions. Future work addressing persistence of exploited marine populations in the face of environmental variability and extremes should expand the spatial and economic aspects of the model to include a more detailed tactical simulation of small-scale spatial heterogeneity in habitat type and quality and variability in reserve spacing (Kaplan and Botsford 2005); realistic dispersal patterns accounting for oceanographic conditions and, when applicable, larval behavior; and the incorporation of a more complex model for the distribution of fishing effort. For example, dynamic closures may be more effective when local population abundances and dispersal patterns vary (Littler et al. 2010). In addition, while adult abalone are generally sedentary, other benthic invertebrates may be capable of moving over distances similar to the patch size modeled here, and adult movement outside MPAs is known to partially reduce the efficacy of protection (Moffitt et al. 2009; De Leo and Micheli 2015).

Despite these caveats, we believe that our analysis is robust and suggests that the interaction of low-frequency, high-risk events and inverse density dependence can unexpectedly raise the risk of collapse for an otherwise sustainably managed species. This model, the first to analyze the benefits of protected areas for managing catastrophic die-off in density-sensitive stock, improves our understanding of the potential disruptive effect of low-frequency, high-risk events when managing under uncertainty and provides a quantitative framework to account for the effects of sudden mass mortality events when balancing persistence and human use in the design of long-term management plans. Allee effects are expected to be common in nature (Kramer et al. 2009), and it is crucial to understand how to improve the resilience of managed species if they are to survive in the face of steadily increasing temperatures (Coumou et al. 2013), acidifying oceans (Hoegh-Guldberg and Bruno 2010), and large-scale extreme events occurring with greater and greater frequency (Coumou and Rahmstorf 2012).

**Acknowledgments**

We thank the Walton Family Foundation, the US National Science Foundation (NSF) Dynamics of Coupled Natural and Human Systems (CNH) program (award DEB-1212124), and the US NSF Ocean Acidification (OA) program (agreement OCE-1416934). We thank members and staff of the fishing cooperative Buzos y Pescadores and of Comunidad y Biodiversidad for their support and advice as well as Greg Dwyer and two anonymous referees for their constructive criticism on early versions of the manuscript.

**APPENDIX A**

**Model Parameters and Equations**

For each patch $x$ of the discretized coastline, following Ellner and Rees (2006), the population density (ind./m²) at
time \( t + 1 \) for a given length \( l \) is described by the following equation:

\[
    n_{z,t}(l) = G(l|l_0)R_{z,t} + \int (S(z, l, t)G(l|l_0))n_{z,t}(l)dl, \tag{A1}
\]

where \( n_{z}(l) \) is the number of individuals of size \( l \) at time \( t \) in patch \( z \); \( R_{z,t} \) is the annual recruits at time \( t \) in patch \( z \); \( L_0 \) is the initial length of recruits; \( G(l|l_0) \) is the growth function, that is, the probability to grow from size \( l_0 \) to size \( l \) in 1 year; and \( S(z, l, t) \) is the survival function, accounting for both size-dependent natural mortality and fishing mortality. Note that initial survival for new recruits is already incorporated into the \( R_{z,t} \) value. Growth, survival, fecundity, dispersal, and catch functions are defined below.

**Growth**

We used a probabilistic nonnegative Gompertz growth function to model annual green abalone growth (Gompertz 1825; Bardos 2005). This function creates a distribution of possible growth increments \( \Delta l \) for any specific starting length \( l \) and avoids negative growth by allowing maximum length \( L_\infty \) to vary dynamically with \( l \). The mean and variance of \( L_\infty \) are determined by \( L_\infty \) and \( \sigma_l \), respectively, with associated scaling parameters \( \beta \) and \( \gamma \). Thus, the probability of an abalone of length \( l \) growing by the length increment \( \Delta l \) is

\[
    G(\Delta l|l) = \frac{\lambda e^{\gamma/(\rho)(L_\infty - l)^{\rho - 1} + \lambda}}{1 - e^{-\lambda\Delta l}} \left(\frac{\Delta l + l}{l}\right)^{1/(\rho - 1)}, \tag{A2}
\]

where \( G \) is the Gompertz growth parameter, \( \Gamma() \) is the gamma function, and

\[
    L_\infty = \left\{(l + \Delta l)^{1/e^{\gamma/(\rho)}}\right\}^{1/(1 - e^{\gamma/(\rho)}),} \tag{A3}
\]

\[
    \lambda = \frac{L_\infty}{\left(1 + (\beta/(L_\infty))^\gamma\right)^\gamma}, \tag{A4}
\]

\[
    \rho = \frac{L_\infty^2/(1 + (\beta/(L_\infty))^\gamma)\gamma}{\left(\sigma_l/(1 + (\gamma/(L_\infty))^\gamma)\right)^2}; \tag{A5}
\]

The five parameters of the Gompertz growth function \( G, L_\infty, \sigma_l, \beta, \) and \( \gamma \) were estimated by Rossetto et al. (2015) by minimizing the following negative log-likelihood function using observed abalone growth data:

\[
    \log(L) = \sum \log(p(\Delta l|l_0)), \tag{A6}
\]

**Survival**

The instantaneous mortality rate \( \mu(l) \) for abalone in natural environments is related linearly to body mass \( w(l) \) (Rossetto et al. 2012), which can be estimated from length (Shepherd 1998):

\[
    \ln \mu(l) = \theta + \alpha \ln w(l), \tag{A7}
\]

\[
    w(l) = a_w \cdot \hat{f}, \tag{A8}
\]

where \( \theta, \alpha, a_w, \) and \( b_w \) are scaling parameters.

We calculated annual survival for an individual in patch \( z \) by integrating instantaneous survival from starting length \( l_0 \) to ending length \( l \), and assuming that all harvest occurs at the end of the year:

\[
    S(z, l_0, l) = \begin{cases} 
        (1 - h) \int_{l_0}^{l} e^{-\alpha \ln w(l)} dl & \text{if } l > L_{\text{min}}, z \in Z_t, \\
        \int_{l_0}^{l} e^{-\alpha \ln w(l)} dl & \text{otherwise},
    \end{cases} \tag{A9}
\]

where \( h \) is the constant annual harvest proportion based on the assumption of constant effort; \( L_{\text{min}} \) is the minimum harvest size, and \( Z_t \) is the set of fished patches (see “Catch” below).

**Fecundity**

The number of eggs produced in each patch \( z \) at time \( t \) is calculated as follows from eggs per unit of mass \( e_n \) and the total mature female biomass (assuming a 1:1 sex ratio) in patch \( z \) (Tutschulte 1976; Rossetto et al. 2013), modified by the Allee effect \( \text{Allee}_{z,t} \):

\[
    E_{z,t} = \text{Allee}_{z,t} \cdot e_n \int p_{\text{mature}}(l)w(l)n_{z,t}(l) dl. \tag{A10}
\]

The proportion of reproductive individuals for a specific length \( l \) is

\[
    p_{\text{mature}}(l) = \frac{1}{1 + \exp((-l - L_{\text{mat}})/a_{\text{mat}})}, \tag{A11}
\]

where \( a_{\text{mat}} \) is a scaling parameter and \( L_{\text{mat}} \) is the length at which half of individuals are mature (Rossetto et al. 2013). The Allee effect in patch \( z \) at time \( t \), \( \text{Allee}_{z,t} \), is determined by mean aggregation size \( \text{Agg}_{z,t} \):

\[
    \text{Allee}_{z,t} = p_{\text{mature}}(\text{Agg}_{z,t}). \tag{A12}
\]

\( \text{Agg}_{z,t} \) is calculated using the total density of mature individuals \( M_{z,t} \):

\[
    M_{z,t} = \int p_{\text{mature}}(l)n_{z,t}(l) dl, \tag{A13}
\]

to estimate mean aggregation size (Button 2008),
Agg_{z,t} = a_{agg} \cdot M_{z,t} + b_{agg}, \quad (A14) 

and is used to determine the probability of mixed gender aggregations:

\[ P_{\text{mixed}}(\text{Agg}_{z,t}) = 1 - 0.5^{\text{Agg}_{z,t}}. \quad (A15) \]

The aggregation regression parameters \( a_{agg} \) and \( b_{agg} \) were derived from Button (2008) by setting the 80% breeding success threshold for the Allee effect to 0.2 mature adults per square meter. This value is similar to that seen in prior work (0.15–0.2 [Shepherd and Brown 1993; Shepherd and Partington 1995] and 0.3 [Babcock and Keesing 1999]) and is consistent with recruitment failure seen in the field (failure at 0.003 vs. success at 0.85; Rogers-Bennett et al. 2004).

**Dispersal, Settlement, and Recruitment**

Larval dispersal was assumed to be Gaussian with a mean dispersal distance \( d(t) \) that varies stochastically from year to year according to a gamma distribution with shape \( \gamma \) and rate \( \delta \). The fraction of larvae dispersing \( k \) patches away from the source patch, with \( k = \pm 1, \pm 2, \ldots \) was thus computed as follows:

\[
\rho(k) = \int_{100k+1/(2)}^{100k-1/(2)} \frac{1}{\sqrt{2\pi\sigma^2(t)}} \exp(-x^2/2\sigma^2(t))dx. \quad (A16)
\]

The number of settlers in patch \( z \) at time \( t \) was calculated summing the contribution of all patches \( j \) as follows:

\[
S_{z,t} = r(t)\sigma_y \sum_j E_{j,t} \rho(|j-z|), \quad (A17)
\]

where \( j \) is the set of patches, \( \sigma_y \) represents the survival from eggs to settlers, and \( r(t) \) is a random variable with mean \( = 1 \) and a lognormal distribution (fig. 2C) that represents relative annual fluctuations in settler survival rate due to year-to-year environmental variability (Szuwalski et al. 2015).

Following Micheli et al. (2008) and Rossetto et al. (2013), we modeled recruitment \( R_{z,t} \) as a Ricker function (Ricker 1954) of the form

\[
R_{z,t} = a_{3,1} S_{z,t} \exp \left( -\frac{S_{z,t}}{K} \right), \quad (A18)
\]

with density dependence occurring only at the settlement stage, carrying capacity \( K \), and \( r(t) \) in equation (A17) accounting for year-to-year environmental variability.

**Catch**

Catch is calculated in metric tons as

\[
C_t = 10^{-6}A \sum_{z_i} \int_{\text{max}}^{t_{\text{final}}} h(z_i,w(l))n_{z_i}(l)dl, \quad (A19)
\]

where \( A \) is the area of each patch and \( Z_i \) is the set of fishable patches (i.e., those that are not set aside as no-take zones). Harvest proportion \( h_z \) is the proportion of commercial size abalone that is harvested from each fishable patch in year \( t \) for management scenario \( x \):

\[
h_z = \begin{cases} 
\frac{2}{3}F_{\text{MSY}} & \text{if } x = \text{NC, DC}, \\
\frac{h_{\text{NC}}}{(1-fp_c)} & \text{if } x = \text{MPA},
\end{cases} \quad (A20)
\]

where \( F_{\text{MSY}} \) is the harvest rate associated with the MSY and \( fp_c \) is the fraction of protected coastline.

**Table A1: Model parameter values**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symbol</th>
<th>Value</th>
<th>Unit</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length at recruitment</td>
<td>( L_0 )</td>
<td>1</td>
<td>mm</td>
<td>a</td>
</tr>
<tr>
<td>Length for 50% maturity</td>
<td>( L_{\text{mat}} )</td>
<td>135.99</td>
<td>mm</td>
<td>a</td>
</tr>
<tr>
<td>Minimum harvest length</td>
<td>( L_{\text{min}} )</td>
<td>155</td>
<td>mm</td>
<td>a</td>
</tr>
<tr>
<td>Annual harvest proportion</td>
<td>( h_x )</td>
<td>Variable</td>
<td>b</td>
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<tr>
<td>Weight scaling value</td>
<td>( a_w )</td>
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<td>g mm^{-3w}</td>
<td>c</td>
</tr>
<tr>
<td>Weight exponent</td>
<td>( b_w )</td>
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<tr>
<td>No-shell weight proportion</td>
<td>( a_{\text{no-shell}} )</td>
<td>Variable</td>
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<tr>
<td>Gompertz growth parameter</td>
<td>( G )</td>
<td>0.5635</td>
<td>d</td>
<td></td>
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<tr>
<td>Gompertz maximum length mean</td>
<td>( L_n )</td>
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<tr>
<td>Gompertz maximum length variation</td>
<td>( \sigma_L^2 )</td>
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<tr>
<td>Gompertz mean scaling</td>
<td>( \beta )</td>
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<tr>
<td>Gompertz variation scaling</td>
<td>( \gamma )</td>
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<tr>
<td>Mortality scaling</td>
<td>( \alpha )</td>
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<tr>
<td>Mortality intercept</td>
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<tr>
<td>Maturity scaling value</td>
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Table A1 (Continued)

<table>
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<th>Symbol</th>
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</tr>
</thead>
<tbody>
<tr>
<td>Fecundity</td>
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<td>eggs g$^{-1}$</td>
<td>f</td>
</tr>
<tr>
<td>Slope for aggregation estimate</td>
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<tr>
<td>Intercept for aggregation estimate</td>
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<td>Survival of eggs</td>
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<tr>
<td>Survival of recruits</td>
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<td>a</td>
<td></td>
</tr>
<tr>
<td>Carrying capacity for recruits</td>
<td>$K$</td>
<td>$1.29 \times 10^7$</td>
<td>individuals</td>
<td>i</td>
</tr>
</tbody>
</table>

Spatial/stochastic:

- Length of coastline: 15,000 m
- Length of block: 100 m
- Width of block: 500 m
- Area of each block: $A = 5 \times 10^4$ m$^2$
- Mean dispersal distance gamma shape: $d_i = 3$ m
- Mean dispersal distance gamma rate: $d_i = .006$ j
- Recruitment lognormal mean: $r_m = 0$ k
- Recruitment lognormal standard deviation: $r_{sd} = .7$ k

---

Literature Cited


Associate Editor: Greg Dwyer
Editor: Judith L. Bronstein

“Previous to the year 1763 bluefish were very plenty on the southern coast of Cape Code, but about this year they all disappeared, and none were taken till sixty or seventy years after. For the past thirty years specimens have been taken, but they did not arrive in any noticeable abundance till within the last sixteen years, and are at the present time again vanishing.” Figured: Above, “The Haddock, Morrhua æglefinus.” Below, “The Bluefish, Temnodon saltator.” From “The Habits and Migrations of Some of the Marine Fishes of Massachusetts” by James H. Blake (The American Naturalist, 1870, 4:513–521).